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PEABODY MUSEUM
OF NATURAL HISTORY
YALE UNIVERSITY

A Comparative Study of the Egg-White Proteins of Passerine Birds

CHARLES G. SIBLEY

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1. Facing page 1. List of Figures, item 28 should read "Thraupini" (not Traupini).
2. Page 11, under "Materials", lines 7-8 should read "... see Acknowledgments page 118....".
3. Page 13, Fig. 1 and page 15, Fig. 2. Add to the legends for these figures: A = application point; C-18 = Component 18 (= Ovomacroglobulin); Tr = Ovotransferrin (= Ovoconalbumin); Om = Ovomuroid; Ov = Ovalbumin; Pre = Prealbumin.
4. Page 44. Urocynchramus is cardueline (not emberizine).
5. Page 97, bottom line, last word, should read "ploceids".

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ABSTRACT

The starch-gel electrophoretic patterns of the egg-white proteins of 668 species of the avian order Passeriformes were studied. Evidence of family level systematic relationships was sought and compared with evidence from anatomy, behavior, etc. In many cases the previously accepted classification was supported, in others questions were raised by the protein data. These include: (1) The New World non-oscine families seem to be more closely related to one another than any one of them is to the Pittidae, Acanthisittidae or other Old World non-oscine families. (2) The Corvidae and Laniidae may be related. (3) The Paradiseidae are probably related to the Cracticidae. (4) *Chamaea* is probably closest to the Sylviidae, not to the Timaliidae. (5) *Psaltiriparus* and *Aegithalos* are closely related to one another and may be closer to the sylviids than to *Parus*. (6) The Timaliidae may be a natural group including *Picathartes* but not including either *Panurus* or *Chamaea*. (7) The Sylviidae and Muscicapidae are closely related to one another but are less closely related to the Turdidae. (8) *Prunella* is closer to the sylviid-muscicapid assemblage than to the thrushes. (9) *Zeledonia* is a "nine-primaried oscine," probably best placed with the paruline warblers, not in the Turdidae. (10) The Nectariniidae and Meliphagidae differ markedly and probably are not closely related. (11) The ploceines and estrildines are related to one another. (12) *Passer* is unlike the ploceids and may be closer to the fringillids. (13) *Vidua* has an egg-white pattern like that of *Passer* and differs from the ploceids in this and other characters. (14) *Fringilla* is closely related to the carduelines as proved by the existence of valid, cage-bred, hybrids. (15) The carduelines are most closely related to the other "nine-primaried oscines," not to the estrildines. (16) The Drepaninines were probably derived from a cardueline ancestor.

ZUSAMMENFASSUNG

Die am Stärke-Gel gewonnenen elektrophoretischen Muster der Eiweiss-Proteine von 668 Arten der Vogelordnung Passeriformes wurden untersucht. Es wurden Beweise systematischer Verwandtschaft auf dem Familienniveau gesucht und mit solchen aus der Anatomie, des Verhaltens, u.s.w. verglichen. In vielen Fällen wurde die vorher akzeptierte Einteilung unterstützt, in anderen wurden Fragen von Seiten der Proteinangaben aufgeworfen. Diese schliessen ein: (1) Die Neuwelt-Familien der Nicht-Oscinen scheinen miteinander näher verwandt zu sein, als jede von ihnen mit den Pittiden, Acanthisittiden oder mit anderen eurasiatischen Familien der Nicht-Oscinen. (2) Die Corvidae und Laniidae könnten verwandt sein. (3) Die Paradiseidae sind wahrscheinlich mit den Cracticidae verwandt.

(4) *Chamaea* steht wahrscheinlich den Sylviiden und nicht den Timaliiden am nächsten. (5) *Psaltriparus* und *Aegithalos* sind miteinander nahe verwandt und dürften den Sylviiden näher stehen als dem *Parus*. (6) Die Timaliidae könnten eine natürliche Gruppe sein, die *Picathartes*, aber weder *Panurus* noch *Chamaea* einschliesst. (7) Die Sylviidae und Muscicapidae sind miteinander nahe verwandt, jedoch entfernter verwandt mit Turdidae. (8) *Prunella* steht den vereinigten Sylviiden-Muscicapiden näher als den Drosseln. (9) *Zeledonia* ist ein "nine-primaried oscine" wahrscheinlich am besten näher die Parulini eingeordnet und nicht unter Turdidae. (10) Die Nectariniidae und Meliphagidae unterscheiden sich deutlich voneinander und sind wahrscheinlich nicht nahe verwandt. (11) Die Ploceinen und Estrildinen sind miteinander verwandt. (12) *Passer* ist den Ploceiden nicht ähnlich und dürfte den Fringilliden näher stehen. (13) *Vidua* hat ein Eiweissmuster wie das von *Passer* und ist von den Ploceiden in diesem wie in anderen Merkmalen verschieden. (14) *Fringilla* ist den Carduelinen nahe verwandt, wie durch die Existenz einwandfreier, im Käfig ausgebrüteter Hybriden bewiesen ist. (15) Die Carduelinen sind den anderen "nine-primaried oscines" am nächsten verwandt, nicht den Estrildinen. (16) Die Drepanininen stammen wahrscheinlich von einem Carduelin-Vorfahr ab.

РЕЗЮМЕ

Были изучены фигуры распределения протеинов белка яиц 668 видов птиц из отряда воробьиных, полученные электрофорезом в крахмальном геле. Искались доказательства родства между семействами; они тоже сравнивались с данными анатомии, наблюдений над поведением птиц и т. д. Во многих случаях ранее принятая классификация подтверждена; в других — данные изучения протеинов возбудили вопросы. Последние включают следующие: (1) Кажется, что семейства Нового Света подотряда Tyranni стоят ближе друг к другу, чем любое из них к Pittidae, Acanthisittidae, или к другим семействам Старого Света. (2) Возможно, что Corvidae и Laniidae родственны. (3) Вероятно, что Paradiseidae родственны с Cracticidae. (4) Вероятно, что *Chamaea* ближе всего к Sylviidae, а не к Timaliidae. (5) *Psaltriparus* и *Aegithalos* тесно родственны друг к другу и возможно, что ближе к Sylviidae, чем к *Parus*. (6) Возможно, что Timaliidae являются естественной группой, включающей *Picathartes*, но не включающей *Panarus* и *Chamaea*. (7) Sylviidae и Muscicapidae тесно родственны друг к другу; но не так близко родственны с Turdidae. (8) *Prunella* ближе к группе Sylviidae-Muscicapidae, чем к дроздам. (9) Вероятно, что лучшее место для *Zeledonia* вместе с Parulini, а не в Turdidae. (10) Nectariniidae и Meliphagidae резко отличаются и, вероятно, близко не родственны. (11) Ploceinae и Estrildinae родственны друг к другу. (12) *Passer* отличается от Ploceidae и может быть ближе к Fringillidae. (13) Электрофоретическая фигура яичного белка у *Vidua* похожа на фигуру у *Passer*; *Vidua* отличается от Ploceidae по этим и другим признакам. (14) *Fringilla* близко родственна с Carduelinae, что подтверждается наличием здоровых гибридов, выращенных в клетках. (15) Carduelinae ближе всего родственны с Fringillidae и их родственниками, а не с Estrildinae. (16) Вероятно, что Drepanines произошли от предка, принадлежавшего к Carduelinae.

INTRODUCTION

The avian order Passeriformes contains more than 5000 of the approximately 8600 species of living birds. The passerines represent a relatively recent radiation of mostly small land-dwelling species adapted primarily to feed upon insects, fruit and seeds, and except for the structures involved in feeding they tend to be anatomically uniform. Thus they present special difficulties when attempts are made to subdivide them into families and genera. Subdivisions based upon the bill and associated characters of the skull run the risk of producing groups composed of unrelated but convergently similar species while the postcranial anatomy provides few trustworthy clues to relationships. One obvious conclusion from these facts is that the members of this order are closely related. This is certainly true and this conclusion introduces the problem of equivalence between a family of passerines and a family of non-passerines. This problem is not new, for Sclater (1880: 345-346) was troubled by the "vexed question of the division of the Oscines into families. The difficulty here obviously arises from the fact that the Oscines are all very closely related to one another, and, in reality, form little more than one group, equivalent to other so-called families of birds. As, however, there are some 4700 species of Oscines known, it is absolutely necessary to subdivide them; and the task of doing this in the most convenient and natural way is not an easy one."

Gadow (1891: 252) also stated the problem clearly when he wrote, "In talking of these 'families' we are apt to forget, or rather we never appreciate, the solemn fact that, strictly speaking, all the Oscines together are of the rank of one family only!" Lucas (1894) also emphasized that the passerines have usually been split into too many families, thus destroying even a semblance of equivalence between passerine and non-passerine families. Fürbringer (1888) recognized only two families of passerines while modern authors divide the same group into as many as 70 (Wetmore, 1960), 50 (Mayr and Amadon, 1951) or 49 (Stresemann, 1934).

To bring passerine and non-passerine families into full equivalence would produce as many new problems as it would solve but at least this disparity should never be forgotten and, when proof of close relationship becomes available, passerine families should be merged. The pivotal word in the previous sentence is "proof" and a cautious and conservative approach is advocated. No changes should be made without the presentation of compelling new information. New data, not merely new arrangements, are needed if real progress toward a stable, natural classification is to be achieved.

The classifications of birds currently in use owe some of their features to history and a complete understanding of present viewpoints would require an analysis of past systems. Although a detailed historical review is outside the boundaries of this paper it is helpful to note a few examples and to mention some of the people who have shaped our thinking and perhaps provided us with our prejudices.

After Linnaeus and Cuvier it was possibly G. R. Gray who exerted the most important early influences upon certain aspects of avian systematics. Gray's *List of the Genera of Birds* (1840) was followed by several editions and culminated in the famous *Hand-list*, the final volume of which was published in 1871. Gray's classification of the passerines was based mainly upon external characters, especially of the bill.

It is possible to find in Gray's list the sources of some arrangements still in use. Whether or not these involve errors is yet to be determined. What is important to understand is that Gray based his groupings and the sequence of his families upon a few superficial characters. Gray's *List* had a lasting influence at least in part because it covered all known species and was a convenient basis for arranging collections and organizing faunal works. However, additional characters were being studied and gradually these new data began to reveal some of the weaknesses in the older systems. Nitzsch (1840) examined the pterylography of many groups and Müller (1847) studied the structure of the syrinx. Müller's work may well be considered the beginning of the modern classification of passerine birds for his major subdivisions are found in all current arrangements. By 1863 Cabanis and Heine (1850–1863) had combined the ideas of Keyserling and Blasius (1839), Nitzsch and Müller into a system which was not extremely different from those in use today. The influence of Darwin stimulated many comparative anatomical studies and the work of Huxley, Garrod, Forbes, Sundevall, Sclater, Fürbringer, Gadow, Sharpe, Seebohm, Parker, Newton, Shufeldt, Lucas, Beddard and Pycraft helped to clarify many problems.

The first volume of what was to be "unquestionably the most important work on systematic ornithology that has ever been published" (Zimmer, 1926: 96) appeared in 1874. The *Catalogue of the Birds in the British Museum* was begun by Sharpe who wrote 13 of the 27 volumes. The passerine volumes (3–15), written by Sharpe, Seebohm, Gadow and P. L. Sclater, were published between 1877 and 1890. The emphasis in the *Catalogue* was upon the description of species and, to a lesser extent, the diagnosis of genera. Families and subfamilies were diagnosed and, in some instances, discussions of family-level relationships were presented. The influence of the *Catalogue* upon later workers would be difficult to overestimate. It became, and to a large extent remains, the point of departure for studies in avian systematics.

By 1880, when Sclater (1880, 1881) presented his cogent "Remarks", the boundaries of the present suborders and families of passerines had been established. Changes since that time have been relatively minor. Sclater recorded his departure from Gray's system and acknowledged his debt to Müller, Nitzsch, Sundevall (1872–73), Garrod, Huxley and others. The classification developed by Stejneger (1885) was based upon that of Sclater and was in turn used by many later systematists.

Although by 1900 the broader outlines of avian classification seemed reasonably clear, it was apparent to some ornithologists that many problems remained. Ridgway (1901–1911) claimed no originality for his classification, basing it upon earlier proposals, but he noted (1901: vii–viii) that "The imperfection of our knowledge concerning the internal structure of many groups of birds, however, makes an entirely satisfactory classification impossible at the present time, and

that here adopted must therefore be considered as provisional only." The difficulties associated with the classification of passerine birds were emphasized by Ridgway as due to the relative lack of gaps resulting from the extinction of intermediate types and also to the unequal distribution of such gaps.

Ridgway's "monumental work . . . is a detailed, taxonomic monograph . . . indispensable to the systematist of North and Middle American ornithology" (Zimmer, 1926: 525). Although some of the planned volumes on the non-passerines are not yet published Ridgway himself wrote the first eight. Parts 1-5 cover the Passeriformes and provide complete, detailed descriptions of all species. What makes Ridgway's work outstanding, and still extremely useful, is that he presented the criteria upon which New World passerines were, and still are, classified. Ridgway included complete citations to previous works and discussions of the taxonomic problems he encountered. He pointed out the weaknesses in the characters he used and he was consistent in providing reasons for his allocations of species and genera. Ridgway's diagnoses and discussions pertaining to the higher categories of passerines are the most complete available and he recorded the discrepancies and difficulties in numerous footnotes.

Interest in the relationships of the orders and families declined somewhat after the turn of the century as more attention was devoted to the lower categories. Among those concerned with passerine family level classification were Clark, Chapin, Lowe and Sushkin. The classifications of Wetmore (1930) and Stresemann (1934), although differing in some respects, were not essentially different from the earlier systems. Wetmore has updated his list at intervals (1934; 1940; 1951; 1960) but the changes have been minor. In 1951 Mayr and Amadon published a classification which reduced the number of passerine families from the 70 of Wetmore (1960) to 50 but otherwise changed little but the sequence of families. Classifications of all or part of the Passeriformes have also been presented by Mayr and Greenway (1956), Amadon (1957), Delacour and Vaurie (1957) and Storer (1960). In all of these the boundaries of families have remained about the same as in the earlier lists.

Through the 'thirties and 'forties interest was directed mainly to problems of speciation and geographic variation. Higher category relationships were given less attention although some authors (e.g., Delacour, 1943a & b, 1944, 1946b; Amadon, 1943, 1944, 1956; Mayr and Amadon, 1947; Mayr and Vaurie, 1948) commented upon the relationships among certain passerine families in the introductory sections of generic revisions.

Then, in 1953, Beecher published his study of the jaw musculature of the oscines and presented extensive new data covering most of the passerine families. Beecher's assumptions and conclusions have been criticized (Tordoff, 1954b; Mayr, 1955; Jollie, 1958; Bock, 1960) but his paper dramatized the nature and extent of the problems and the depth of the uncertainties about passerine relationships. Beecher's willingness to propose new and unexpected groupings helped to re-open the entire question of passerine classification and to stimulate further studies. Tordoff (1954a, b) investigated the relationships of the "finches" and certain other oscines basing his study primarily upon a comparison of the "palato-maxillaries". His conclusions were at first accepted (Mayr, 1955) but later Bock disagreed. From an extensive study Bock (1960: 470) concluded that

the palatine process of the premaxilla is of "little or no value in showing relationships between families of passerine birds or in placing problem genera in the correct family."

The taxonomic value of other characters has also been challenged. Berger (1956a) demonstrated that the *expansor secundariorum* muscle is actually present in all birds and thus cannot be used as a basis for diagnosing the passerines as Garrod (1876a) had done. The scutellation of the tarsus, which has been used to diagnose certain groups of passerines, has been found to be unreliable by Pycraft (1906), Blaszyk (1935), Plotnick and Pergolani de Costa (1955), Rand (1959) and Ames, Heimerdinger and Warter (1968). Although Ridgway (1907) used tarsal scutellation to define some groups, he recorded the difficulties he encountered in a footnote (p. 336) in which he stated that he had been disappointed in the hope that the classification of the Tyrannidae might be simplified by the use of the characteristics of the tarsal envelope. He found instead that "they seem of little value beyond the definition of genera (even sometimes failing here!) or minor supergeneric groups; indeed, it has been found that each of them is more or less variable within what appear to be proper generic limits."

Heimerdinger and Ames (1967) found the suboscine sternum to be a highly variable structure and recommended caution in the use of sternal characters in taxonomy. Feduccia (1967) has shown that the amphirhinal condition of the nares in the passerines is extremely variable in occurrence and is not reliable as a taxonomic character. Attempts to apply observations of behavior patterns to taxonomic problems have had variable success. Ficken and Ficken (1966), Andrew (1961), Löhrl (1964) and Nicolai (1964), among others, have based taxonomic suggestions upon behavior.

Additional anatomical studies and several novel techniques have also been applied to these old problems. Bowman (1961) carried out a study of the diet, feeding behavior and feeding structures in the Galapagos finches; Stegmann (1962) examined the condition of the outer primary, the number of primaries and the shape of the wing; George (1962) studied the bones and muscles of the hyoid apparatus in many passerines; Stresemann (1963) questioned several assumptions concerning the number of primaries; Bock (1962b) determined the condition of the pneumatic fossa in the head of the passerine humerus; Heimerdinger (1964) studied passerine pterylography; Ames (1965) studied the passerine syrinx; Ziswiler (1964, 1965, 1967a, b) compared the feeding behavior and associated structures in seed-eating birds; Stephan (1966) determined the number of secondaries in the passerines; and Pocock (1966) compared certain osteological characters in several passerine groups.¹ Ackermann (1967) applied numerical taxonomic methods to a study of the skeleton of several seed-eating passerines. He concluded that numerical taxonomy is "of doubtful value, at least for systematic ornithology," but that it may be useful as an auxiliary method.

¹ While this paper was in press C. J. O. Harrison (1969. Additional information on the carpometacarpal process as a taxonomic character. Bull. Brit. Ornith. Club 89: 27-29) published some observations on one of the characters discussed by Pocock (1966). Harrison's general conclusion is that Pocock's "process D" on the carpometacarpus is actually quite variable and that "when used as a single character the taxonomic value of this process is uncertain."

Stallcup (1954) used both myology and serology in a study of the Fringillidae and (1961) serology in a comparison of several passerine families. McFarlane (1963) compared the structure of the spermatozoa in several families and Norris (1963) presented some data on the blood group reactions of passerine birds. The data of Stallcup and Norris are of uncertain significance for systematics while McFarlane's material is still too limited to judge its value.

The success of comparative studies of chromosome morphology in plant taxonomy has been impressive, especially at the lower categorical levels, but karyological studies on birds have not been successful. Udagawa (e.g., 1954, 1955, 1956, 1957) and Baldwin (1953a) have been among those attempting to obtain data from this source. Mainardi, in a long series of papers (e.g., 1957 a, b, c, 1958, 1960, 1961) has used immunological and biochemical techniques in comparative studies of several passerine groups.

At the present time, we have several different classification schemes which differ but slightly from one another. For the most part the differences involve the categorical levels to be utilized for a group (family vs. subfamily) and the sequence of families in a linear list (Mayr and Greenway, 1956; Wetmore, 1957; Delacour and Vaurie, 1957; Mayr, 1958; Storer, 1959). Although these classifications are similar the authors would, I am sure, agree that they are "provisional only" and that there remain many uncertainties about the actual relationships of the groups. In this paper I will attempt to review the pertinent literature on passerine classification and to present from a study of the egg-white proteins some new data bearing upon the problems of family level relationships.

PROTEIN MOLECULES AS A SOURCE OF DATA FOR CLASSIFICATION

THE SYNTHESIS, STRUCTURE AND PROPERTIES OF PROTEINS

The rationale underlying the search for evidence of genetic relatedness in the structure of homologous proteins from different species has been discussed in several previous papers (Sibley, 1960, 1962, 1964, 1965, 1967). In summary, the argument is based upon the now established facts that genetic information is encoded in the sequence of nucleotides in the genetic material, DNA, and that this sequence is translated, during the synthesis of protein molecules, into a corresponding sequence of the 20 kinds of amino acids of which proteins are composed. Thus protein molecules are genetic messages and, by a commonly accepted definition, a gene (or cistron) is the sequence of nucleotides which codes for a single polypeptide chain. A protein molecule is composed of one or more polypeptide chains.

The sequence of the amino acids which are linked together by peptide bonds forms the *primary* structure of a polypeptide chain. In many proteins the *secondary* structure of the chain is the helical twist—the *alpha helix*—which at least some segments of the chain assume. This helical structure confers greater rigidity upon the chain. The *tertiary* conformation is achieved when the polypeptide chain folds upon itself in a specific fashion determined by the relationships of the side chains of the amino acids and hence by their sequence. The tertiary configuration is often stabilized by disulfide bridges between two cysteine residues and by non-covalent bonds of several types. Many proteins are composed of a single polypeptide chain. Others, for example hemoglobin, are composed of more than one chain. The organization of the chains of a multi-chain protein constitutes its *quaternary* structure.

Proteins are large molecules with molecular weights usually in the range from 10,000 to 200,000 and even up to a million. For example, the egg-white proteins of the domestic fowl (*Gallus gallus*) include lysozyme which is a single chain of 134 amino acids with a molecular weight of 14,800 and ovalbumin which contains nearly 400 amino acid links and has a molecular weight of 45,000. Ovoconalbumin (or ovotransferrin) has a molecular weight of 76,600 and contains nearly 800 amino acids while ovomucoid has a molecular weight of 28,000 and contains about 200 amino acids.

Another property of proteins is that of net charge which is the algebraic sum of the charges on the amino acids. The principal contributors to the electric charge of a protein are the ionizable groups of the side chains of lysine, arginine, glutamic acid, aspartic acid and histidine. The carboxyl and amino groups at the ends of the polypeptide chain also contribute to the net charge. Because the charge on these ionizable groups is *pH* dependent, the net charge of a protein varies with the *pH* of its environment. Thus a protein can be negative, neutral or positive in charge depending upon the *pH* of the solution in which it is

placed. The *pH* at which a protein has a net charge of zero in a particular buffer is its *isoelectric point*. For example, the lysozyme of the domestic fowl (*G. gallus*) is isoelectric at *pH* 10.7, ovalbumin is isoelectric at *pH* 4.6, ovoconalbumin at *pH* 6.8 and ovomucoid at *pH* 3.9.

Proteins possess many other properties but size and charge are of particular importance in relation to the characterization of proteins using electrophoretic techniques.

THE TECHNIQUE OF ELECTROPHORESIS

Electrophoresis is defined as "the movement of charged particles suspended in a liquid under the influence of an applied electric field." The usual procedure involves the placement of a mixture of proteins, such as blood plasma, avian egg white, etc. at a standard point on a supporting substance, for example, a strip of filter paper, a gel of starch or a membrane of cellulose acetate. The supporting material is saturated with a buffer solution and so arranged that a direct current can be passed through it. Because proteins are charged particles they will move in an electrical field at a speed which is primarily a function of the net charge on the molecule. In some gel systems the pores of the gel matrix may be small enough to retard the movement of protein molecules in proportion to their size, thus introducing an index to molecular weight and shape as well as net charge. This is true of the starch gel method used in this study.

Because the different proteins in a mixture like egg white have different charges and are of different sizes they will migrate at different speeds. Those with a net negative charge will move anodally, those with a positive charge cathodally and those with a charge of zero will not move at all. Larger molecules will be slowed more by a gel matrix than will small molecules. The result will be that, after a period of electrophoresis, the different kinds of proteins in the mixture will be separated along the axis of the current. If the supporting material containing the proteins is then placed in a solution containing a dye which bonds only to proteins, the positions and relative amounts of the different proteins in the mixture can be seen. The resulting patterns can then be compared in the same way that other morphological characters are compared.

Following is a technical description of the conditions under which the electrophoretic patterns used in this study were produced.

The technique of vertical starch gel electrophoresis (Smithies, 1955; 1959a, b) with a discontinuous buffer system (Poulik, 1957) as modified by Ashton and Braden (1961) and Ferguson and Wallace (1961) was used. The starch gel buffer was composed of 0.046 *M* Tris [= tris (hydroxymethyl) aminomethane], 0.007 *M* citric acid, 0.005 *M* lithium hydroxide and 0.019 *M* boric acid at a *pH* of 7.95. The "bridge" buffer consisted of 0.05 *M* lithium hydroxide and 0.19 *M* boric acid, *pH* 7.98. Electrophoresis was effected by a constant current of 35 ma, at voltages from 400–600 volts, until a bromphenol blue dye marker line had moved 8 cm anodally from the application slots. This required from 4–5 hours. All gels were run in a cold room at 4° C. Following electrophoresis the gels were removed, sliced horizontally and stained for total protein with Amido Black

10 B. Destaining was accomplished by successive washings in 2½% (v/v) acetic acid and the stained patterns were then photographed in transmitted light using 4" × 5" Eastman "Panatomic X" (ASA 64) film and a Wratten G-15 deep yellow filter.

The iron-binding ovoconalbumins were identified by incubating one half of the sliced gel with 2, 4-dinitroso-1, 3-naphthalene-diol (Canal Industrial Corp., Bethesda, Md.), a specific stain for iron.

MATERIALS

Between 1956 and 1968 approximately 12,000 specimens of avian egg white from over 1000 species have been assembled. About half of the specimens and at least 668 species represent passerines. Specimens have been obtained from 60 of Wetmore's (1960) 70 passerine families. The 10 groups not represented are the Oxyruncidae, Philepittidae, Atrichornithidae, Ptilonorhynchidae, Hyposittidae, Chloropseidae, Vangidae, Prionopidae, Callaeidae and Catamblyrhynchidae.

The specimens were collected by many persons [see Acknowledgments in Sibley and Ahlquist, (in press)] in many parts of the world under various conditions.

In the course of this study approximately 6,000 samples, of which 2,800 were of passerine origin, have been analyzed by electrophoresis in starch gel. The patterns reproduced in this paper have been chosen from a large number of examples. From some common species numerous samples have been examined and certain especially interesting samples have been re-run many times either to provide side by side comparisons with the egg-white proteins of other species or to obtain improved patterns.

THE INTERPRETATION OF ELECTROPHORETIC PATTERNS

There are several sources of variation in electrophoretic patterns which can alter the appearance of a pattern but which are not important in assessing the taxonomic significance of similarities and differences between patterns. Unless this problem is understood, and due allowances for such variations are made, it is impossible to make useful comparisons between patterns.

TAXONOMICALLY NON-SIGNIFICANT VARIATION

The most important sources of non-significant variation are denaturation, sample concentration and artifacts due to the experimental procedure.

DENATURATION. This term covers various processes which result in minor alterations of proteins. Such changes may result from a slight degree of relaxation of the three-dimensional configuration of the molecules, or other modifications which affect the behavior of the protein during electrophoresis. Heat is especially likely to cause minor damage which often results in a loss of sharp definition in the electrophoretic pattern of one or more of the egg-white proteins. The

ovoconalbumins (ovotransferrins) seem to be especially susceptible to denaturation and thus they frequently appear as a blurred region or they may disappear completely. Figure 1 illustrates the type of change usually caused by denaturation.

When better specimens were available I have avoided the use of denatured material but in some cases only damaged specimens could be obtained. Since these can usually be relied upon to indicate many of the important features of a pattern they have been used and if one understands and allows for their limitations they can provide valid comparisons. For example, although the discrete banding of the ovoconalbumins may be lost, their approximate position will usually be indicated by a stained, although blurred, area. Similarly, the sharp bands that often appear in the ovalbumin region in fresh material may become a solid, stained area in a denatured specimen.

SAMPLE CONCENTRATION. The intensity of the stained areas in the electrophoretic patterns varies with the concentration of the protein solution used. It might seem preferable to use a single, measured concentration but a more complete understanding of a pattern is obtained by using a series of dilutions. This is because the different proteins in avian egg white occur naturally in different concentrations. Thus a dilute specimen permits one to determine the true nature of the pattern in the ovalbumin region and a concentrated sample reveals minor components which are not visible in the dilute specimens. By combining the information from different concentrations, and from many species, it is possible to determine the true pattern of a group and to realize that a series of patterns, no two of which superficially appear to be the same, are essentially identical. In effect such judgments are no different from those based upon the examination of many museum skins in various stages of wear and molt.

Figure 1 indicates the changes in appearance which result from different sample dilutions.

ARTIFACTS. There are several effects which result in artifacts. For example, the fast moving ovalbumins have a tendency to spread out laterally when there is no protein in the adjacent channel. I have avoided the use of such patterns in the plates but it is because of this phenomenon that two channels have been used for each specimen. This insures a clear boundary between them.

Heating of the gel during electrophoresis can also distort the pattern. This has been avoided by running all gels in a cold room.

In many patterns component 18 has a streaked or smeared appearance. This is an artifact but the cause is uncertain.

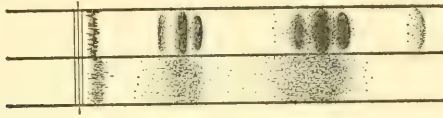
The egg-white protein ovoconalbumin binds such metals as iron, copper and zinc. Ovoconalbumin molecules containing bound iron migrate faster than those lacking iron. The resulting small mobility difference is an artifact (Baker, 1968).

In some patterns there are spots or streaks which result from a variety of sources. If they are not obviously part of the pattern they can be assumed to be artifacts.

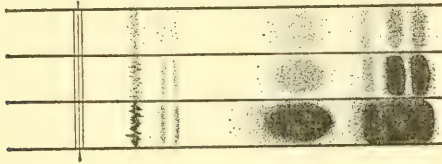
TAXONOMICALLY SIGNIFICANT VARIATION

After allowances have been made for variations due to denaturation, sample concentration and artifacts there remain some real differences among the egg-

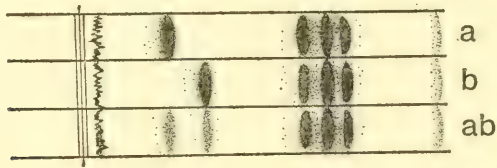
Denaturation



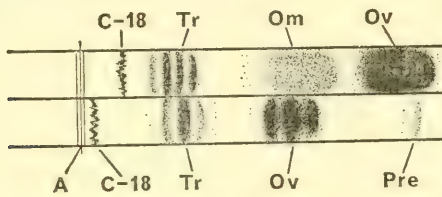
Sample concentration



Polymorphism



Differences in number



Differences in mobility

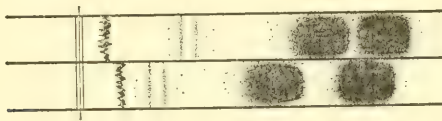


FIGURE 1. Some sources of variation in electrophoretic patterns and their effects. Denaturation: pattern of undenatured egg white above, denatured below. Sample concentration: dilute sample above, optimal concentration middle, concentrated sample below. Polymorphism: samples from three individuals of the same population showing three ovoconalbumin phenotypes, a, b, and the heterozygote ab. Differences in the number of proteins in two species. Differences in the mobilities of homologous proteins in two species.

white protein patterns of many groups of passerines. These differences are due to variation in the number and in the mobility of proteins.

DIFFERENCES IN NUMBER OF PROTEINS. The presence or absence of apparently homologous² proteins constitutes an important character in the electrophoretic patterns. Such differences suggest that the genetic basis for the protein is also present or absent. At least we must assume this to be the case unless proved to the contrary.

In some cases a difference in mobility may result in an apparent difference in the number of proteins. For example, the presence of an "ovomucoid" in "Type B" patterns and its apparent absence in "Type A" patterns is probably due to a mobility difference. In "Type A" patterns the "ovomucoid" fraction is probably present but because it has a mobility close to that of the ovalbumin the two fractions tend to merge and thus appear as one. This problem is discussed on p. 20 under "The Pattern Types."

Variation in the number of proteins may also be due to genetic polymorphism. This is especially frequent in the ovoconalbumins (= ovotransferrins) and Brush (1968) has reviewed the literature and presented data on the variation in the conalbumins of the red-winged blackbird (*Agelaius phoeniceus*). Although this type of variation is of great interest and significance, especially at the species level, it does not seem to provide a useful basis for speculation about the relationships of the higher categories. Therefore, in the present paper, I have not utilized differences or similarities in the number of the conalbumins as important taxonomic characters.

DIFFERENCES IN THE MOBILITIES OF PROTEINS. Variation in the mobility of a homologous protein in different species is frequently observed. Reference to Fig. 2 and to the figures illustrating actual starch gels (figs. 3-38) will provide examples. Presumably such differences in mobility are caused by differences of one or more amino acids and thus a real genetic difference is indicated. Mobility differences contribute to the similarities and differences we observe when comparing electrophoretic patterns. To assess the taxonomic significance of variation in mobility it seems best to consider each of the major fractions separately. Baker (1968) has reviewed the literature on egg-white proteins, most of which pertains to non-passerines.

Component 18 (Ovomacroglobulin) shows remarkably little variation within a given group and this consistency suggests that when differences are observed they may be significant. For example, the Corvidae have a relatively fast component 18 while that of the "nine-primaried oscines" (= Fringillidae of this paper) tends to be slow. Other groups fall between these extremes.

Ovoconalbumins often show quite striking mobility differences but the tendency for the conalbumins to exhibit polymorphism makes it difficult to assess the significance of such differences. If the conalbumins occur consistently in one

² In this paper the definition of homologous as applied to proteins agrees with the statement of Nolan and Margoliash (1968: 728) as follows: "Homologous, in accordance to its common biological usage, would imply that the genes coding for the polypeptide chains considered, in all the species carrying these proteins, had at one time a common ancestral gene and have evolved independently since their original divergence."

region of the pattern in all species of a group it is reasonable to assume that this is a significant character. In the Corvidae, for example, they occur close to component 18; in other groups they are found about midway between component 18 and the faster fractions; and in the Meliphagidae and some other groups they migrate just behind the fastest fractions. As noted above, the mobilities of the conalbumins change slightly in relation to the amount of iron which is bound by the protein.

"Ovomucoid", "Ovalbumin", and "Pre-albumin". The proteins in avian egg white were first isolated and named in studies of the egg-white proteins of the domestic fowl (*Gallus gallus*). They have been identified in other non-passerine birds but the homologs of ovomucoid, ovalbumin and pre-albumin have not been definitely identified in passerine egg white although it is reasonable to assume that they are present. The greatest uncertainty, in my opinion, concerns

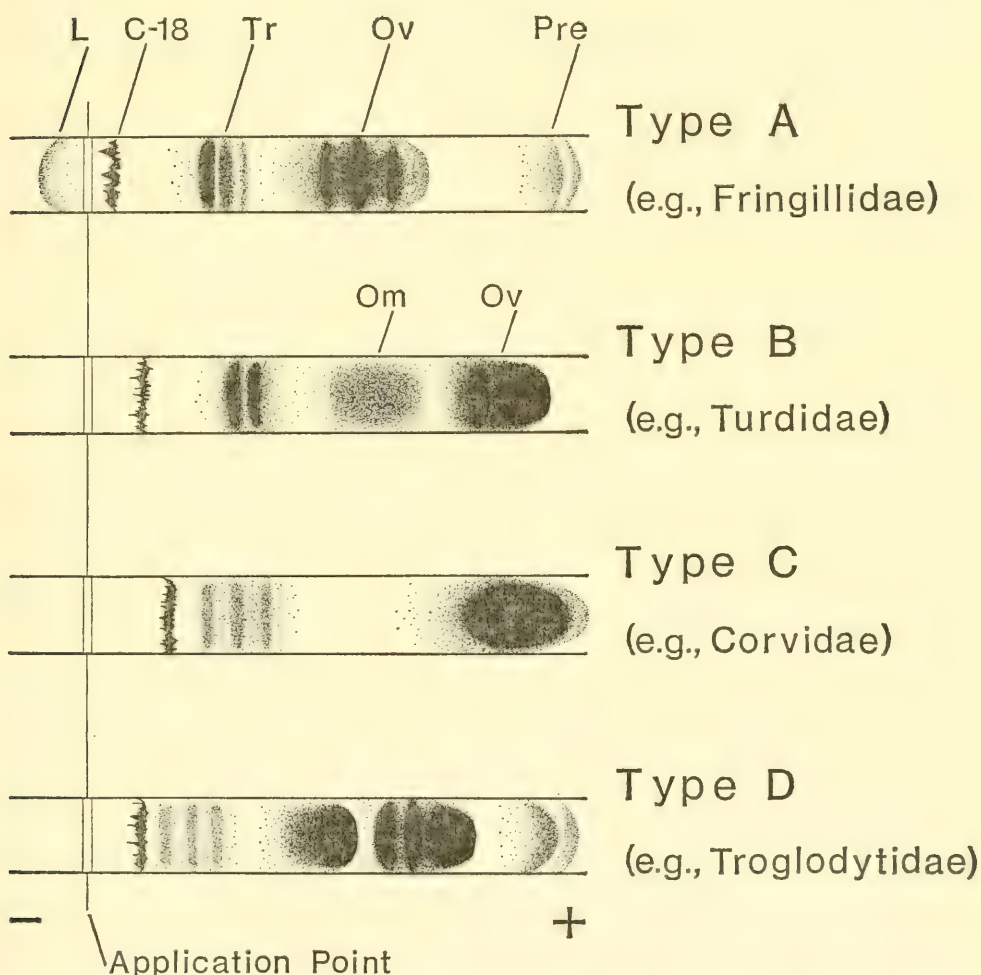


FIGURE 2. The four major types of starch gel electrophoretic patterns produced by the egg-white proteins of passerine birds.

the ovomucoid fraction. To indicate this lack of positive identification between the ovomucoid of the domestic fowl and the electrophoretically similar fraction in many passerine egg whites I have enclosed the word in quotation marks. This uncertainty about the homologies of these fractions does not affect their significance as components of electrophoretic patterns.

There is a tendency for these fast fractions to have similar mobilities within a group of closely related species. Many examples can be seen in the plates. Small changes in the mobility of one of the fast fractions can alter the pattern considerably and herein lies one of the major problems of interpretation. For example, in most of the Turdidae there is a clear separation between the "ovomucoid" and "ovalbumin" bands, but in concentrated samples of *Sialia* there appears to be but a single fast fraction because the mobilities of the two proteins are so similar that they merge. In dilute samples the two separate fractions can be seen. In summary, when comparing electrophoretic patterns it is necessary first to assess the effects of denaturation, sample concentration and possibly polymorphism. By making appropriate allowances for these factors it is possible to determine the typical pattern for a group of related species.

Comparisons should seek to assess the magnitude of significant qualitative and quantitative differences. The greatest weight should be given to qualitative differences, especially the presence or absence of major components. Differences in electrophoretic mobility and in the amount of a protein present should be accorded less weight in making comparisons.

THE TAXONOMIC SIGNIFICANCE AND LIMITATIONS OF ELECTROPHORETIC DATA

The previous sections have discussed the following:

- 1) Protein molecules are synthesized on a genetically determined template.
- 2) The sequence of amino acids composing a protein chain is the genetically determined property of a protein.
- 3) The electrophoretic behavior of a protein molecule is primarily a function of its net charge and, in some gel systems, of its molecular size and shape.
- 4) Electrophoretic patterns are affected by several variables which can alter their appearance and make their interpretation difficult. The effects of denaturation, sample concentration and artifacts are not important in the evaluation of patterns relative to higher category relationships; differences in the number of proteins are most important, mobility differences somewhat less so.

From these facts it follows that, although genetically significant information is encoded in the sequence of the amino acids in a protein, electrophoretic behavior reflects only net charge and molecular proportions. What then is the taxonomic significance of differences and similarities between the starch gel electrophoretic patterns of avian egg-white proteins and what pitfalls must be

avoided? The answers to these questions can best be developed by considering the following problems.

ELECTROPHORETIC COINCIDENCE

It is clear, from the foregoing sections, that two proteins having different amino acid sequences could have the same net charge and the same molecular weight. They could therefore have the same electrophoretic mobility and would not be distinguished by electrophoretic examination. However, although electrophoretic coincidence is theoretically a serious problem, it is likely to be a hazard only when comparisons are made between single proteins of unknown homologies. It is not likely to present a serious problem when comparisons are made between complex systems of homologous proteins, such as avian egg white. Fortunately, when electrophoretic coincidence seems likely, it can be tested by such additional methods as serological identification or the examination of the specific peptides produced by, for example, tryptic digestion (Sibley, 1964, 1967; Sibley, Corbin and Haavie, 1969).

CONVERGENCE

Convergence in protein structure must be defined as the situation in which two proteins now having identical or nearly identical amino acid sequences were derived from separate genetic lineages which had different sequences in the past. Two such proteins might have identical properties and would possibly be indistinguishable. How great is this hazard?

There are several lines of evidence that suggest that it is a negligible problem and can safely be ignored.

First it may be noted that even a short sequence of the 20 kinds of amino acids can occur in an astronomical number of permutations. For example a sequence of seven can occur in over a billion different arrangements. It therefore becomes highly improbable that sequences of a hundred or more amino acids will come to be identical unless they have had a recent common ancestor and thus were nearly identical to begin with.

A second point that bears upon this problem is that the amino acid sequences of many proteins are remarkably conservative. The enzyme cytochrome *c* of vertebrates, for example, contains 104 amino acid residues in a single chain and the complete sequences are known for several species. There are differences between the cytochromes *c* from different organisms but the similarities are even more impressive. The domestic fowl (*Gallus gallus*) and the turkey (*Meleagris gallopavo*) have identical cytochrome *c* amino acid sequences. The cytochrome *c* sequence of these two galliform birds differs from that of the domestic duck (*Anas platyrhynchos*) at three positions, from that of the king penguin (*Aptenodytes patagonica*) at two positions, from the snapping turtle (*Chelydra serpentina*) at eight positions, and from that of the great grey kangaroo (*Macropus kanguru*) at eleven positions. In each comparison the remainder of the 104 positions are identical. Cytochrome *c* is found in nearly all organisms and at least 22 complete sequences are known. Bakers' yeast (*Saccharomyces*) has 108 amino acids in its cytochrome *c* chain and 64 of these occupy positions

identical to those in human cytochrome *c*. There are several identical segments between the human and yeast chains including sequences of 5, 6, 8 and 11 amino acids. The sequence of 11 has been so strongly conserved that it has not been found to vary in any of the 22 species so far studied. These include fungi, yeast, wheat, insects and various vertebrates (Dayhoff and Eck, 1968). These authors have noted (p. vii) that "Because of their unexpectedly great conservation through geological time, proteins effectively represent millions of different 'living fossils' containing detailed information about their origin and history. One topic of great interest which will certainly be worked out through protein studies is the exact relationship and order of derivation of the living kingdoms and phyla." They could, with equal cogency, include the remainder of the taxonomic categories.

Zuckerlandl and Pauling (1965: 161-164) have presented another important argument. It seems highly probable that protein evolution proceeds via the process of gene duplication as the first step. One of the two resulting duplicate genes is then free to incorporate mutations which can lead to new functions while the other copy continues to code for the original protein which performs the original function. The alternative to this process would be for the original gene itself to change by the incorporation of mutations. If this occurred frequently the probability of convergence is obviously greatly increased. Zuckerlandl and Pauling argue that it is improbable that the intermediate structures produced during this process would be functional and hence retained by natural selection. They therefore conclude that "the ease with which variations of a given type of protein can be produced through duplication and mutation of a gene should be so much greater than the ease of convergent evolution from independent starting points that on the basis of this consideration alone any variants within a given type of tertiary structure and function seem to have a much greater chance to be phyletically related than unrelated."

For those interested in a more detailed review of these and related problems the papers by Dixon (1966), Nolan and Margoliash (1968) and Watts (1968) provide a convenient entry to an extensive and growing literature on protein evolution.

True evolutionary convergence in amino acid sequences then can be assumed to be unlikely and the hazard of electrophoretic coincidence is a minor problem when comparing systems of homologous proteins such as avian egg white. However, electrophoretic patterns do not provide an index to the sequence of amino acids in proteins. How then is it possible to invest electrophoretic patterns with taxonomic significance and what precautions must be observed to avoid conclusions that exceed the ability of such patterns to indicate genetic relationships?

INTERNAL STANDARDS FOR COMPARISONS

The patterns produced by electrophoretic characterizations of avian egg-white proteins provide an index to the net charges, sizes and possibly shapes of the several proteins in the system. These properties do not vary at random but are apparently restricted by the primary structure of the proteins, the amino acid

sequence. Thus, although electrophoretic properties do not directly indicate the sequence, they are to some degree controlled by it. Evidence of this control is found in the impressive similarity of electrophoretic patterns which is observed when the egg-white proteins of a group of closely related species are compared. Among the passerines there are many examples; in fact, nearly every family can be cited as demonstrating that closely related birds have similar or identical egg-white protein electrophoretic patterns. Some families provide especially convincing proof. For example, the available species of the Corvidae, although of world wide distribution, have an essentially identical egg-white protein electrophoretic pattern. That they are a closely related, monophyletic group is attested by the impressive similarities in a large array of characters, including the skeleton (Ashley, 1941), jaw muscles (Beecher, 1953), behavior and external morphology (Amadon, 1944). Similarly, the New World nine-primaried oscines (= Fringillidae of this paper), which are a morphologically variable group but clearly of monophyletic ancestry, show a remarkable degree of similarity in their egg-white protein patterns. Other examples could be cited. The point is that the existence of this high degree of similarity among closely related but genetically isolated species, indicates that electrophoretic patterns reflect the basic evolutionary conservatism of protein structure. The existence of such similar patterns among related species thus provides an internal standard for the interpretation of the taxonomic significance of the patterns. Clearly the confidence we are justified in placing in such an internal standard is directly proportional to the number of species which are available for study from a given group. It has taken many years to build up a collection of comparative material of sufficient size to provide a high degree of confidence for at least some of the passerine assemblages. The lack of material from enough species to establish an internal standard for some groups has made it difficult to develop conclusions or suggestions concerning the significance of their egg-white protein patterns.

The application of the internal standard is simple and direct. A species that departs markedly from the pattern type which is found in several other species of a group is immediately suspect and becomes the object of further study. Such departures may reflect minor differences due to a single amino acid substitution but they could also be a clue to a case of convergence in gross morphology which has led to an incorrect assignment to a higher category. There are several examples in the present study including the genera *Acanthiza*, *Chamaea* and *Panurus*. The true relationships of *Zeledonia* were discovered when its egg-white pattern was found to match those of the wood warblers and to differ from those of the thrushes (Sibley, 1968).

The establishment of internal standards as the basis for judging the taxonomic value of electrophoretic patterns is thus no different than for any other character. The criteria for a useful character are that it be similar or identical in closely related species and that it differ between less related species. The electrophoretic patterns meet this requirement better than most other characters because they are so impressively similar within related groups. Among the passerines the differences between less closely related groups are sometimes striking and readily defined. In other cases groups which have previously been

thought to be unrelated turn out to have similar patterns. These similarities may be due to close relationship but the hazard of electrophoretic coincidence must also be considered and tested before any conclusions are presented.

THE PATTERN TYPES

During this study of the electrophoretic patterns of passerine egg-white proteins it gradually became clear that most of the variations in the patterns could be assigned to one of at least four major types. These types, designated "A", "B", "C" and "D", differ in the number of separate visible fractions and in the mobilities of homologous proteins. It is important to recognize that a change in mobility may change the number of visible fractions. This occurs when two proteins which are visibly separate in one species have similar or identical mobilities in another. In the second species the pattern will seem to lack a fraction present in the first species but the missing protein actually may be present but hidden because it has the same mobility as another major component. For example, a study of the egg-white proteins of *Sayornis* (Tyrannidae), *Turdus* (Turdidae), and *Passer* (Passeridae) has shown that the "ovomucoid" fraction, which is visible in the patterns of *Sayornis* and *Turdus*, also occurs in the pattern of *Passer* in which it merges with the ovalbumin region. Presumably all passerine egg whites contain an "ovomucoid" fraction. Thus the principal difference between "Type A" and "Type B" patterns is due to a change in mobility, not to the presence or absence of a protein. Since the genetic significance of a mobility difference is presumably less than that underlying the gain or loss of an entire protein we must conclude that the taxonomic significance of the differences between "Type A" and "Type B" may be relatively small. Nevertheless, because there do exist consistent similarities within groups of related species, and consistent differences between the members of different groups, we are justified in suspecting that such clusters may be natural assemblages.

Diagrams of the four pattern types are presented in Figure 2 and they may be described as follows.

Type A. A relatively simple pattern which lacks a separate, visible "ovomucoid" and has a fast, usually faint, pre-albumin. The ovalbumin shows several bands in dilute samples but these tend to merge into a single large region in more concentrated samples. The ovalbumin tends to be relatively slow, thus the densely staining portion of the pattern tends to be short, although the pre-albumins often extend well beyond the ovalbumin.

Examples: *Sylvia*, *Muscicapa*, *Parus*, *Certhia*, *Meliphaga*, Fringillidae, *Passer*, etc.

Type B. Distinguished from Type A by a strong "ovomucoid" component between the conalbumins and the ovalbumin. Usually a longer pattern than Type A because the ovalbumin has a faster mobility. As in Type A the ovalbumin region shows several bands in dilute samples but the "ovomucoid" usually seems to be a single, rather diffuse component. There are

usually no pre-albumins but it should be noted that the ovalbumin region in most Type B patterns has approximately the same mobility as the pre-albumins in many Type A patterns. This observation bears upon the problem of the homologies among passerine egg-white components.

Examples: *Turdus*, *Pycnonotus*, *Sturnus*, *Nectarinia*, *Ploceus*, *Estrilda*, *Sayornis*, etc.

Type C. Resembles Type A in lacking a visible "ovomucoid" but has a very fast component 18 which is usually close to the conalbumins.

Examples: Corvidae, *Lanius*, *Campephaga*.

Type D. Resembles Type B in having a visible "ovomucoid" but also has strong pre-albumins and a fast component 18.

Examples: Troglodytidae.

Frequent reference to the pattern types is made in the text, primarily for descriptive purposes. It is not assumed that different passerine groups having similar patterns are necessarily related but the possession of similar patterns is considered to be of sufficient importance to raise the question of possible relationship. The "groups" delineated by the pattern types are defined and discussed in the Discussion and Summary, p. 109-117.

AIMS AND VIEWPOINTS

The presentation of the material in this paper follows a reasonably standard format for each taxonomic unit. The introductory sections preceding the non-oscines and the Passeres include synoptic reviews of the history of the classification of the groups and of the principal characters upon which suborders, superfamilies and families have been based. Similarly, the history of the opinions concerning the relationships of the families is reviewed under each family. This procedure presents the reader with a summary of previous opinions. For the most part I have not attempted to evaluate the evidence upon which these opinions were based because this leads to a far more complex account and because the conflicting opinions themselves demonstrate how difficult it is to interpret the various kinds of evidence available to us.

In the reviews of data and opinions from other sources and in the evaluation of the comparisons of the electrophoretic patterns of the egg-white proteins I have sought for evidence of the degrees of "genetic relatedness" among the taxa of passerine birds. The term "genetic relatedness" may be taken to be a synonym of "phylogenetic" when used in the sense defined by Mayr (1965: 79) who noted that "when a biologist speaks of phylogenetic relationship, he means relationship in gene content rather than cladistic genealogy." To some systematists however, the word phylogenetic means the historical or genealogical dimension and it is to avoid this misunderstanding that I have adopted "genetic relatedness." In addition, a classification based upon genetic relatedness should have greater predictive value than one based upon cladistic genealogy because it will reflect the degrees of genetic difference which have been achieved rather than how long it took to achieve them. However, genetic relatedness

and cladistic genealogy are not mutually exclusive and there are promising data from protein structure (Nolan and Margoliash, 1968) that suggest that the rate of protein evolution may offer a basis for the dating of the branching points in the history of living groups.

This paper then is primarily concerned with the search for evidence of the degrees of genetic relatedness among living passerine birds. In some instances I have felt that the evidence supports the classification currently in use and in a few instances the evidence supports a proposal to modify that classification. In other cases new questions or doubts are raised. Such questions and doubts provide the stimulus for additional research.

I agree with Throckmorton (1968) that "evaluations of characters, of character states, and of groups are probability estimates (improbable, probable, highly probable, etc.)" and that "phylogenetic taxonomy cannot produce absolute answers." I am skeptical about the ability of the available data of all kinds to *prove* very much about the genetic relationships of the higher categories of birds but this does not mean that I think that all characters are equally informative. My skepticism is reflected in the use of terms reflecting a judgment of relative probabilities including "suggest," "indicate," etc. and in the avoidance of "proof" or "proved."

The electrophoretic patterns of the egg-white proteins reflect certain morphological characters of protein molecules. They suffer from some of the same shortcomings we find in other characters but they also represent new evidence pertaining to the "vexed question" of the relationships of passerine birds. They also represent another step on the long road to full utilization of the enormous amount of evolutionary information which is encoded in the structure of protein molecules.

THE NON-OSCINE PASSERINES (SUBORDERS EURYLAIMI AND TYRANNI)

HISTORICAL REVIEW OF THE CLASSIFICATION OF THE NON-OSCINE PASSERINES

To obtain some historical perspective it may be useful to review some of the studies which have contributed to the development of the present classification of the non-oscines, an assemblage which Stresemann (1934: 845, transl.) has characterized as "this by no means natural group."

The presently accepted major divisions of the Passeriformes are based upon characters of the syrinx which were discovered by Johannes Müller (1847). Müller was the first to recognize the tracheophones as a group and he placed all of the New World forms under a single heading. He also separated the Tyrannidae from the Muscicapidae on the basis of syringeal structure.

Following Müller the principal taxonomic contributions began with Garrod (1876b) who reported on the syrinx of *Pitta* and designated it as mesomyodian. He also noted the deep temporal fossae and believed them to be unique in the passerines. The main artery of the leg was also considered in this paper and the greater development of the sciatic artery in the Tyrannidae, *Pitta* and *Rupicola* was noted in contrast to the femoral artery in the Pipridae and Cotingidae. Upon this basis Garrod removed *Rupicola* from the Cotingidae.

Garrod (1877a) also reported the existence of the distinctive vinculum in the foot of the Eurylaimidae and noted that some species of the Dendrocolaptidae are schizorhinal while others are holorhinal. Nevertheless he used the condition of the nares to divide his Tracheophonae into families, including separate families for the Furnariidae and Dendrocolaptidae. In a later paper (1877b) the syringes of cotingas and manakins were found to be similar and Garrod thought that only differences in tarsal scutellation separated the two groups.

The next studies were those of Forbes (1880a) who confirmed Garrod's findings on the vinculum in the Eurylaimidae and established the mesomyodian nature of the syrinx. Forbes (1880b) also described the syrinx of *Philepitta* and noted that in its detailed structure it was quite different from all the other haploophones, although by definition it is tracheo-bronchial. In 1882 Forbes published on *Xenicus* and *Acanthisitta*, allying them to the haploophone families on the basis of the syrinx while noting many differences in other anatomical characters.

Sclater (1880) and Newton (1884) adopted the conclusions of Garrod and Forbes as did Coues (1884), Stejneger (1885) and others.

The great work of Fürbringer (1888) gave little new or special information on the non-oscines and the conclusions of Müller, Garrod and Forbes were apparently followed. In 1891 Sharpe published his masterly "Review" and included his own classification which essentially followed Slater, hence Garrod and Forbes.

Gadow (1893) was the first in many years to make some significant changes and to question some of the accepted arrangements. Gadow believed (p. 272) that neither the number of syringeal muscles nor the distinction between the meso- and acromyodian conditions were useful criteria. He regarded the Pittidae as a link between the Eurylaimidae and the other Clamatores and he thought that the Acanthisittidae (Xenicidae) were close to the pittas. Gadow also believed that the Tracheophonae and the Tyrannidae were closely related and he placed the manakins and cotingas in the Tyrannidae, *Conopophaga* in the Pteroptochidae (= Rhinocryptidae) and made a single family (Formicariidae) of the rest of the tracheophones. He was the first to suggest that the New World groups were probably related to one another and to imply that there was no proof of their relationship to the Old World groups, regardless of the condition of the syrinx.

Gadow also wrote the section on the syrinx in Newton's (1896) *Dictionary* and dared to challenge the orthodox view by claiming to see indications of "a tracheophonous syrinx . . . in various Cotingidae and Pittidae" (p. 940).

Beddard (1898) described many variations in syringeal structure but followed the scheme of Garrod and Forbes for the classification of the non-oscines.

Ridgway (1901) disagreed with Gadow's (1893) arrangement and allied the Clamatores with the oscines rather than with the Eurylaimidae, thus following Garrod and Forbes at the subordinal level. In 1907 Ridgway used Haploophonae and Tracheophonae as group names, but not as formal categories, although the prime dichotomy in his family key is on the basis of syringeal position.

Pycraft (1905a) felt that the skull of the Acanthisittidae agreed with that of *Synallaxis* (Furnariidae) sufficiently to ally these two groups in spite of syringeal differences and suggested that the Acanthisittidae should occupy a place between the Pipridae and the tracheophones. He also thought the Tyrannidae to be closer to the Pittidae than to the tracheophones. A modification of Garrod's system was proposed by Pycraft (1906) to include the Xenicidae (= Acanthisittidae) in the suborder Tracheophonae in spite of its haploophone syrinx and lack of a processus vocalis. Pycraft believed *Conopophaga* was unrelated to the Furnariidae but allied to the Formicariidae, a view recently supported by Heimerdinger and Ames (1967) and Ames, Heimerdinger and Warter (1968).

Pycraft (1907) continued his osteological studies and proposed that the Cotingidae, Pipridae and Philepittidae should be allied with the Eurylaimidae in one suborder while other suborders included, 1) the tracheophones, 2) the Tyrannidae, Phytotomidae and Pittidae, and 3) the oscines.

Clark (1913) made an anatomical study of *Oxyruncus* and concluded that it is a tyrannid. The long paper by Köditz (1925) yields little relating directly to the present question. Rüppell (1933) described the syrinx of the woodcreeper *Lepidocolaptes* and Küchler (1936) made a complete anatomical study of *Phytotoma* from which he concluded that the plant-cutters belong in the Cotingidae.

Even this brief and incomplete historical synopsis indicates that disagreements have been numerous and that evidence from different sources has been conflicting. The present classification is based upon the original work of relatively few workers and often upon rather scanty material. Müller examined the syringes of one or two species in each of about 30 genera and Garrod

and Forbes studied approximately 20 additional species, mainly of groups not available to Müller. Ridgway (1907: 329) called attention to the fact that the internal anatomy of most species is merely assumed to be like that of the few related ones which have been dissected. Thus some of the present feeling of confidence in the accepted arrangement may rest upon the fact that it has been accepted and repeated by so many for so long. It is obvious that the syringeal characters provide an excellent basis for classification and the family boundaries may be the limits of natural groups, although some might well be merged. However, the assumption, based upon the position of the syrinx, that the presently accepted superfamilies are valid may be open to question. There is reason to suspect that at least some of the New World groups are probably as closely or more closely related to one another than any one of them is to the Pittidae, Philepittidae or Acanthisittidae. It is therefore of special interest to note that the extensive study of the syrinx by Ames (1965), in which many additional species were examined for the first time, provides the basis for both agreement and disagreement with the classifications of Wetmore (1960) and Mayr and Amadon (1951). A discussion and outline of Ames' study follows the next section on the present classification.

THE PRESENT CLASSIFICATION

The two classifications currently most used (Mayr and Amadon, 1951; Wetmore, 1960) agree upon the principal subdivisions of the non-oscine passerines. They disagree only upon the rank (family vs. subfamily) of two groups and upon the sequence of families. The following synopsis, using Wetmore's arrangement, would be generally acceptable today.

ORDER PASSERIFORMES.

SUBORDER EURYLAIMI.

FAMILY EURYLAIMIDAE, Broadbills.

Tendon of flexor hallucis connected by a vinculum to tendon of flexor profundus (Garrod, 1877a); toes 3 and 4 joined basally; tarsi with scutes on anterior surface and small 6-sided scales posteriorly; 15 cervical vertebrae; 10 primaries (Stegmann, 1962: 68); 12 rectrices; paired carotids at least in *Pseudocalyptomena* and possibly others; main artery of the leg is the ischiatic; non-furcate spina sternalis; simple syrinx which is mesomyodian, i.e. the intrinsic syringeal muscles (if present) attach to one end or to the middle of the bronchial half-rings.

SUBORDER TYRANNI (Mesomyodes or Clamatores).

Passeriformes without plantar vinculum; left carotid only; 14 cervical vertebrae; tarsal scutellation variable; syrinx mesomyodian.

SUPERFAMILY FURNARIOIDEA (Tracheophonae).

Syrinx tracheophone; processus vocalis usually present.

FAMILY DENDROCOLAPTIDAE, Woodcreepers.

Two pairs of intrinsic (tracheo-bronchial) muscles; sternum 2-notched;

tarsus endaspidean; nares holorhinal; three anterior toes united for full length of basal phalanx and middle toe fused to outer also at level of second phalanx; outer toe as long as middle toe, much longer than inner toe.

FAMILY FURNARIIDAE, Ovenbirds.

Syrinx, sternum and tarsus essentially as in Dendrocolaptidae; nares schizorhinal; outer toe shorter than middle toe, middle and outer toes united basally.

The woodcreepers and ovenbirds are often united in one family (von Ihering, 1915; Stresemann, 1934; Mayr and Amadon, 1951)

FAMILY FORMICARIIDAE, Antbirds.

Usually one pair of intrinsic (tracheo-bronchial) muscles, two pairs in some; sternum usually 2-notched but *Melanopareia* has a 4-notched sternum (Mayr and Amadon, 1951); tarsus taxaspidean; nares holorhinal; basal phalanx of middle toe united to lateral toes; maxilla uncinat and with a subterminal notch.

FAMILY CONOPOPHAGIDAE, Gnateaters and Ant-pipits.

No intrinsic syringeal muscles; sternum 4-notched; tarsus exaspidean; bill flattened; palate schizognathous (all other passerines are aegithognathous); nostrils without operculum.

FAMILY RHINOCRYPTIDAE, Tapaculos.

One pair of intrinsic syringeal muscles; sternum 4-notched; tarsus taxaspidean; nares holorhinal; nostrils operculate; bill shape variable.

SUPERFAMILY TYRANNOIDEA (Haploophonae).

Syrinx haploophone.

FAMILY COTINGIDAE, Cotingas, Bellbirds, etc.

Syrinx catacromyodian (= intrinsic syringeal muscles inserted on ventral ends of bronchial half rings); tarsus variable but never exaspidean; main artery of the thigh is the femoral except in *Rupicola* in which it is the sciatic (Garrod, 1876b).

FAMILY PIPRIDAE, Manakins.

Catacromyodian; main thigh artery the femoral; tarsus exaspidean; second phalanx of middle toe partly coherent to outer toe, or (*Piprites*) the first phalanx of middle toe wholly coherent to inner toe; bill short, broad at base, subterminal maxillary notch.

The cotingas and manakins are sometimes united in one family. Garrod (1877b) believed that only the difference in tarsal scutellation could be used to separate them. Newton (1893) noted that the cotingas have one pair of intrinsic syringeal muscles while some manakins have one pair, others two pairs.

FAMILY TYRANNIDAE, Tyrant Flycatchers.

Syrinx usually said to be anacromyodian (= intrinsic syringeal muscles inserted on the dorsal end of the bronchial half-rings) but Gadow (1893) considered the syringeal structure to be variable. Newton (1893: 939) noted that the number of intrinsic syringeal muscles varies, one in some, two in others; tarsal scutellation usually exaspidean but variable (Ridgway, 1907: 336; Rand, 1959); bill usually flattened and uncinat; nostrils usually rounded and non-operculate or, if narrow and operculate with operculum membranous, not cornuous; rectal bristles usually present.

FAMILY OXYRUNCIDAE, Sharpbills.

Similar to the Tyrannidae in most characters but bill acute, cuneate, with maxilla not uncinat; nostrils narrow, overhung by a broad, corneous operculum; tarsus exaspid; feet relatively stouter.

The sharpbill is sometimes united with the Tyrannidae as a subfamily (Mayr and Amadon, 1951) but Wetmore (1960) believes that its affinities may not be with the Tyrannidae.

FAMILY PHYTOTOMIDAE, Plant-cutters.

Catacromyodian; main thigh artery the sciatic; tarsus pycnaspid; bill stout and conical with serrated tomla.

FAMILY PITTIDAE, Pittas.

Large temporal fossae extending across occipital region of skull, nearly meeting in the midline; tarsal envelope entire and smooth in front (= bilaminat plantar tarsi); intrinsic syringeal muscles usually absent but one pair reported in *Pitta angolensis* which are small, lateral, and attached to the middle of the second bronchial half-ring (= mesomyodian); sciatic is main thigh artery (Garrod, 1876b).

FAMILY ACANTHISITTIDAE (Xenicidae), New Zealand Wrens.

One pair of intrinsic syringeal muscles; tarsal envelope with anterior scutes and long solid "boot" behind (= ocreate); nares schizorhinal; 10 very short rectrices; long, slender maxillo-palatines; bill subulate, acute.

Forbes (1882) thought the haploophone syrinx allied this group to the manakins, pittas, etc., but Pycraft (1905a) placed the Acanthisittidae close to the Furnariidae because of the schizorhinal nares and slender maxillo-palatines. He suggested that the Acanthisittidae belong between the Pipridae and the Tracheophonae.

FAMILY PHILEPITTIDAE, Asities, False Sunbirds.

Intrinsic syringeal muscles expanded at lower insertion and not attached to the bronchial half-rings which are peculiarly modified; tarsal envelope composed of rectangular scutes disposed in regular series; 12 rectrices; tongue penicillate.

Forbes (1880b) considered the syrinx to be mesomyodian and haploophone but the syrinx of *Philepitta* is quite unlike that of the other haploophones. Forbes noted that the syrinx of *Philepitta* is similar to that of the Eurylaimidae.

SUBORDER MENURAE.

Diacromyodian (= intrinsic syringeal muscles attached to both ends of the bronchial half rings); two or three pairs of intrinsic muscles; no plantar vinculum.

FAMILY MENURIDAE, Lyrebirds.

Three pairs of intrinsic syringeal muscles; tarsus taxaspid; sternum with a single, shallow notch; furcula complete but lacking a hypocleideum; 10 primaries (Stegmann, 1962: 68), 10 secondaries, 16 rectrices.

FAMILY ATRICHORNITHIDAE, Scrub-birds.

Two pairs of intrinsic syringeal muscles; tarsus taxaspid; sternum with a single, deep notch; clavicles rudimentary, not forming a furcula; 10 primaries, 12 rectrices.

It is apparent from this brief synopsis of a few characters that, although there is a certain consistency to the classification based upon the position of the syrinx the other characters are not consistent and even the syringeal characters are frequently variable. Pycraft (1906), Blaszyk (1935), Plotnick and Pergolani de Costa (1955), Rand (1959) and Ames et al. (1968) have cast so much doubt upon the taxonomic value of tarsal scutellation at the family level that one is justified in regarding it as untrustworthy. The development of the sciatic as the main artery of the thigh in *Rupicola*, regarded as significant by Garrod (1876b) has been considered to be correlated with a highly specialized behavior pattern by Mayr and Amadon (1951). The Pittidae and Acanthisittidae differ from the other haploophones in a number of characters (Garrod, 1876b; Forbes, 1882; Pycraft, 1905b) and yet they have long been placed in a zoogeographically improbable alliance with the New World Tyrannoidea. Pycraft (1905a) placed the Acanthisittidae with the tracheophones, near the Furnariidae, because he chose to emphasize the taxonomic value of the schizorhinal nares. However, Hofer (1955) and Jollie (1958) have produced evidence that the condition of the nares is a functional characteristic related to several variables and of doubtful taxonomic value. Heimerdinger and Ames (1967) found that the four-notched sternum is not confined to the Rhinocryptidae and *Conopophaga*, as previously believed. Considerable variation in sternal notches was found and correlations with flight patterns were noted.

Modifications in bill and foot structure, in the number of remiges and rectrices, in palatal characters and, in fact, in all of the characters cited in the foregoing synopsis have more or less obvious adaptive significance. Most of them are seldom mentioned in the diagnoses of these groups because there are exceptions to virtually all of them. Thus the syringeal characters have come to be the principal basis for the presently accepted classification.

AMES' STUDY OF THE SYRINX

A synopsis of the classification suggested by Ames (1965) and by Ames, Heimerdinger and Warter (1968) follows:

ORDER PASSERIFORMES.

SUBORDER EURYLAIMI.

Syrinx simple, spina sternalis non-bifurcate.

FAMILY EURYLAIMIDAE, Broadbills.

FAMILY PHILEPITTIDAE, Asities, etc.

Transferred to the Eurylaimi from the Tyranni because the syrinx resembles, in its simplicity, the syrinx of the Eurylaimidae.

SUBORDER TYRANNI.

SUPERFAMILY FURNARIOIDEA.

Syrinx dorso-ventrally compressed; membrane tracheales and processus vocales present; pessulus absent; syringeal musculature variable; lacrymals usually fused to ectethmoid plate; sternum, tarsal scutellation and pterylosis variable.

FAMILY DENDROCOLAPTIDAE, Woodcreepers.

"Horns" on processi vocales; two pairs of intrinsic syringeal muscles; ventral pteryla distinctive.

FAMILY FURNARIIDAE, Ovenbirds.

No "horns" on processi vocales except in *Geositta*; two pairs of intrinsic syringeal muscles; pterylosis unlike that of other suboscines but similar to most oscines.

FAMILY FORMICARIIDAE, Antbirds.

Group 1. Typical antbirds. One pair of intrinsic syringeal muscles; processus vocalis very small; M. sternotrachealis bifurcate near its insertion. Examples: *Taraba*, *Dysithamnus*, *Thamnophilus*, *Myrmotherula*.

Group 2. Ground antbirds. No intrinsic syringeal muscles; processus vocalis large; M. sternotrachealis simple. Examples: *Grallaria*, *Chamaeza*, *Formicarius*, *Conopophaga*.

Heimerdinger and Ames (1967) and Ames, Heimerdinger and Warter (1968) recommend the dissolution of the Conopophagidae by the transfer of *Conopophaga* to the Formicariidae and of *Corythopsis* to the Tyrannidae. The pterylosis of *Conopophaga* is similar to that of *Grallaria*; the pterylosis of *Corythopsis* is like that of the tyrannids.

FAMILY RHINOCRYPTIDAE, Tapaculos.

A single, dorsally originating intrinsic muscle or no intrinsic muscle (*Tele-dromas*); pattern of ventral pteryla, except in *Melanopareia*, is distinctive; lacrymals partly fused.

SUPERFAMILY TYRANNOIDEA.

Syringeal structure variable but basically cylindrical, not dorsoventrally compressed; pessulus usually present; syringeal musculature highly variable; lacrymals free; pterylosis relatively uniform; sterna mainly with single pair of notches; tarsal scutellation variable.

FAMILY COTINGIDAE, Cotingas.

Group 1. Lack intrinsic syringeal muscles (except the bellbirds) and internal cartilages.

Group 2. Have M. obliquus ventralis and internal cartilages. Four genera, currently placed in the Cotingidae, fall into this group, namely, *Attila*, *Casiornis*, *Laniocera* and *Rhytipterna*. Ames (1965) transferred these four genera to the Tyrannidae and divided his first group into five subfamilies under the Cotingidae: Cotinginae (typical cotingas); Pyroderinae (fruit crows); Querulinae (lesser fruit crows); Procnatiinae (bellbirds); and Rupicolinae (cocks-of-the-rock). Each of these subfamilies is characterized by syringeal characters.

FAMILY PIPRIDAE, Manakins.

Variable syringeal structure. *Piprites* resembles certain small tyrannids in the structure of the syrinx, otherwise the manakins show little syringeal similarity to typical tyrannids or cotingids.

FAMILY TYRANNIDAE, Tyrant Flycatchers.

Variable syringeal structure but, with few exceptions, M. obliquus ventralis and internal cartilages are present. Rarely M. obliquus lateralis is present.

Within the Tyrannidae Ames (1965) recognized seven groups based on variations in the syrinx.

FAMILY OXYRUNCIDAE, Sharpbills.

Ames (1965: 255) notes that *Oxyruncus* "has a number of distinctive structural features and appears to merit family status."

FAMILY PHYTOTOMIDAE, Plant-cutters.

Syrinx similar to some cotingas, particularly *Heliochera*.

FAMILY ACANTHISITTIDAE, New Zealand Wrens.

FAMILY PITTIDAE, Pittas.

These two Old World families were considered by Ames (1965) as probably not related to the New World tyrannoids.

FAMILY PHILEPITTIDAE, Asities, etc.

As noted above, Ames transferred this family to the Eurylaimi.

SUBORDER MENURAE, Lyrebirds and Scrub-birds.

Atrichornis not examined by Ames but published accounts suggest that the syringes of *Menura* and *Atrichornis* differ in several ways.

SUBORDER PASSERES or "oscines".

"The extreme homogeneity of the oscine syrinx strongly supports the present inclusion of the sixty-odd families in a single suborder" (Ames, 1965: 266).

One of the impressive aspects of Ames' study is his discovery of the remarkable amount of variation in the syringeal structure of the non-oscines. A major section of the thesis is concerned with this aspect (p. 157-239) and with the relations between structure and function. Essentially all aspects of the syrinx are found to vary, many of them within the higher categories and some even within species. The subject is complex and cannot be reviewed briefly but it is clear as Ames (p. 205) notes, that the "reliance on the syrinx as an overriding character in subdividing the Passeriformes must give way to the use of a number of characters considered in regard to their functional relationships."

The relation between syringeal structure and vocalization is not yet entirely clear but Ames suggested (p. 214) that "In general terms, birds with simple syringeal musculature sing simple songs; those with more complex musculature sing more intricate songs." Ames also noted that the singing ability of the lyrebirds and the oscines may depend more upon "changes in the nervous system, rather than in syringeal structure" (p. 215).

Ames also considered the relationship between plumage colors and voice as signal characters used for species recognition. For example, in the Pittidae, he noted that "Their simple syringeal structure reflects their use of bright colors rather than vocalizations in species recognition" (p. 250), and the typical cotingas, most of which lack intrinsic syringeal muscles, tend to "rely on structural and chromatic elaborations of the feathers for species recognition and courtship" (p. 251).

The large amount of morphological variation in the syringeal structure of the non-oscines compared with the relative uniformity of the syringes of the oscines seems to suggest that to achieve diversity in vocalization with fewer than six pairs of syringeal muscles requires modifications in other elements of the

syrinx. This interpretation would also suggest that in the oscines the more complex syrinx has made it possible to achieve vocal diversity at the level of neural control. If this is the case it would be appropriate to view the variation in non-oscine syringes as, at least in part, a reflection of variation in vocalizations.

Another aspect of this problem is that of deciding how to define "complexity" in songs. Greenewalt (1968: 180) defines complexity as "a phrase or song with elaborate modulations." On this basis Greenewalt notes that the non-oscine tyrannids have songs as complex as those of the oscines. The song of Traill's flycatcher (*Empidonax traillii*), for example, contains modulations as complex as those in any single phrase of the song of the song sparrow (*Melospiza melodia*). However, as Greenewalt states, "the song sparrow has far greater variety in its songs than any of the Tyrannidae, but variety and complexity are not synonymous since a single complex phrase must surely require as elaborate anatomical features as would be needed to produce a number of such phrases." Greenewalt concludes that "only one generalization can be made to distinguish the Oscines from the non-Oscine groups; the frequency range for the Oscines is much greater" and, "the syringeal embellishments characteristic of the Oscines contribute little more than the ability to sing over a greater frequency range, and even here the presence or absence of intrinsic syringeal muscles may be more important than the number of pairs which are present."

Greenewalt's conclusions are based upon an acoustical analysis of many passerine songs but "variety" (frequency range and form of the fundamental) may be more important biologically than "complexity" as defined by Greenewalt. Eugene Morton (personal communication) suggests that sound variety is probably important in the life of a song sparrow but not in that of a flycatcher. This suggestion is supported by the fact that there is virtually no variation in the song of Traill's flycatcher across North America (Stein, 1963) but that it is perhaps impossible to find two song sparrows with identical repertoires (Mulligan, 1966).

The papers by Stein (1968) and by Chamberlain, Gross, Cornwall and Mosby (1968) provide additional facts which will help to determine the relationships between patterns of vocalization and variation in syringeal structure. As noted by Stein (1968: 242), such studies "should not only provide an understanding of the action of the syringeal components, but also provide a better understanding of the taxonomic usefulness of syringeal anatomy."

THE EGG-WHITE PROTEIN DATA

In the following accounts of families frequent reference is made to the four main types of electrophoretic patterns (A, B, C, D) which are found among the egg-white proteins of passerine birds. These have been discussed above under "Pattern Types."

In a few instances reference is made to "disc gel" patterns, for example under the Rhinocryptidae. This refers to electrophoretic patterns produced by the technique described by Ornstein (1964) and Davis (1964) in which a polyacrylamide gel is used as the supporting medium. Between 1960 and 1963 several

thousand "disc gel" separations were prepared as part of this study of passerine egg-white proteins. For side by side comparisons however, the starch gel technique has certain advantages, hence the "disc" patterns will not be published. They have nevertheless contributed importantly to my understanding of the problems discussed in this paper.

The word "ovomucoid" is placed in quotation marks because there is no certainty that the fraction so designated is homologous to the ovomucoid of the domestic fowl (*G. gallus*). It merely occurs in the same relative position in the electrophoretic pattern. The homologies of the fractions herein designated as ovalbumin and pre-albumin are also uncertain. The most anodal fraction occurring in a high concentration has been designated as ovalbumin. Pre-albumin is defined as a component of low concentration occurring ahead of (= more anodal) the ovalbumin. The discussion of the patterns in *Prinia* (p. 71) indicates the nature of this problem.

In the heading of each family account the fraction, e.g. 2/14, indicates the number of species from which egg-white specimens have been examined out of the total number of species assigned to the group by Mayr and Amadon (1951). Also indicated are the plate numbers for the electrophoretic patterns of the egg-white proteins of species considered under each family.

SUBORDER EURYLAIMI.

FAMILY EURYLAIMIDAE, Broadbills, 2/14, fig. 3.

Species examined: *Psarisomus dalhousiae*, *Smithornis capensis*.

Gray (1869-71) placed the broadbills among the non-passerines near the rollers, todies, motmots and trogons. Wallace (1856) suggested that they are the Old World representatives of the Cotingidae. Sclater (1872) agreed with Wallace's suggestion and found that the sternum is typically passerine. The palate was found to be passerine by Garrod (1877a) who also discovered the plantar vinculum, a character that is unique among the Passeriformes. Forbes (1880a), in a study of the Eurylaimidae, confirmed Garrod's observations on the vinculum and described the syrinx in two genera. Forbes (1880b) found several resemblances between *Philepitta* and the broadbills but kept them separate mainly because of the lack of the plantar vinculum in *Philepitta*. Seeböhm (1890) discussed the characters of the Eurylaimi and concluded that they warranted recognition as a suborder of passerines. Gadow (1893) thought the broadbills were related to the pittas while Fürbringer (1902) concluded from a study of the pectoral girdle that the broadbills are most closely related to the Piciformes and also to the swifts, but not to the rollers. Pycraft (1905b), after a comparative study of the skeleton, musculature, pterylosis and syrinx, supported Fürbringer in part and disagreed in part with Forbes. Pycraft thought his evidence indicated that the broadbills are related most closely to the cotingas and perhaps should be included as a subfamily of the Cotingidae. At the same time he thought it possible that the Eurylaimidae would prove to be related both to the goatsuckers and to the swifts.

The possibility that the African genus *Smithornis* is a broadbill was first expressed by Bates (1914) who noted the vinculum and the simple syrinx. Lowe (1924) confirmed Bates' suspicion and later (1931) concluded that *Pseudocalyp-*

tomena is also a broadbill. Lowe (1926) observed that the quadrate of *Eurylaimus* resembles that of *Tyrannus*.

The egg-white protein patterns of *Psarisomus* and *Smithornis* are like one another although there are differences in the mobilities of some components. The patterns of the broadbills are unlike those of *Pitta* in the "ovomucoid"-ovalbumin region and they also differ from those of the Piciformes and the swifts. The broadbill patterns resemble those of the cotingas (*Platyptaris*) and tyrannids but not any more closely than those of several other groups.

I conclude that the broadbills are not closely related to the pittas and because of ample anatomical evidence to the contrary the resemblances to the New World groups cannot be considered important.

SUBORDER TYRANNI.

SUPERFAMILY FURNARIOIDEA.

FAMILY DENDROCOLAPTIDAE, Woodcreepers. 1/47, fig. 3.

Species examined: *Glyphorhynchus spirurus*.

FAMILY FURNARIIDAE, Ovenbirds. 18/212, fig. 3.

Species examined: *Geositta cunicularia*; *Furnarius rufus*; *Leptasthenura aegithaloides*; *Synallaxis ruficapilla*, *azarae*, *frontalis*, *albescens*, *brachyura*; *Certhiaxis cinnamomea*; *Cranioleuca pyrrhophia*; *Asthenes humicola*, *baeri*, *modesta*; *Phacellodomus rufifrons*, *striaticollis*; *Coryphistera alaudina*; *Phylidor rufus*; *Sclerurus caudacutus*.

The starch gel pattern of *Glyphorhynchus* is similar to those of the furnariids, differing from some in the mobility of certain fractions but no more so than the furnariids differ among themselves. The *Glyphorhynchus* sample was in unusually good condition and shows more detail than many of the furnariid specimens. It has a strong band between the conalbumins and the "ovomucoid" region which is barely visible in the better furnariid patterns. This gives the pattern of *Glyphorhynchus* a different appearance but it seems likely that the true patterns of *Glyphorhynchus* and the furnariids are very much alike. If there is a real difference between the two groups additional specimens of dendrocolaptid egg white will be required to prove it.

Feduccia (personal communication) has found a difference between some dendrocolaptids and some furnariids in the electrophoretic mobility of their hemoglobins. I have confirmed Feduccia's observations independently. Feduccia has also noted skull characters which correlate with the hemoglobin evidence and, taken together, these data suggest that, as presently constituted, the two families may be polyphyletic. Feduccia will report upon his studies elsewhere and will suggest certain modifications of the present arrangement.

The starch gel patterns of the furnariids are, for the most part, extremely similar to one another except for variation in mobilities and variation due to the effects of denaturation and sample concentration. Component 18 migrates relatively rapidly in comparison with many passerines and the conalbumins tend to be quite close to component 18. In this the furnariids differ from the formicariids. In most furnariid patterns (*Leptasthenura* may be an exception) the "ovomucoid" and ovalbumin regions are well separated, usually appearing as two dense areas. In dilute samples the ovalbumin region is seen to be com-

posed of two or three fractions. In *Geositta*, for example, three can be seen. One or two pre-albumin bands occur in most of the better samples, as clearly seen in the pattern of *Geositta*. In other species the pre-albumins are often represented by a smeary, stained region ahead of the ovalbumin but in several patterns clear bands are present.

Once the basic pattern has been worked out by a study of all patterns it becomes clear that all of the furnariid patterns are actually much alike. The differences among them are due to small mobility differences, to variation in the condition of the specimens and to the effects of differing dilutions.

Comparisons between the patterns of the Furnariidae and the Formicariidae reveal some consistent differences and several similarities. As noted above, the conalbumins of most of the furnariids migrate close to component 18 but those of the formicariids are consistently almost exactly halfway between component 18 and the "ovomucoid" region. In one pattern of the furnariid *Asthenes baeri* the conalbumins are also halfway between component 18 and the "ovomucoid" region.

As described above, in the furnariids the "ovomucoid" and ovalbumin regions are distinctly separate. In the formicariids these two regions tend to merge in more concentrated samples. However, in dilute specimens, such as *Thamnophilus doliatus* in gel S-239, it is clear that the true formicariid pattern is similar to that of the furnariids. In gel S-418 moderately dilute samples of *Thamnophilus doliatus* and *Furnarius rufus* were run side by side. In these the components 18 have nearly identical mobilities and the differences noted above in the mobilities of the conalbumins are clearly demonstrated. The "ovomucoid" of *Thamnophilus* migrates faster than that of *Furnarius* and thus tends to merge with the ovalbumin region which has the same mobility in both. Each also has two pre-albumin bands which usually are difficult to see in the photographs. Thus these two groups do show some fairly marked and reasonably consistent differences in the mobilities of at least two regions but they share a similar total pattern. This suggests that each is a definable group, separable from the other, but that they are also probably related to one another. The degree of this relationship remains uncertain but it seems to be greater than that between either of these New World groups and any Old World group.

Comparisons between the furnariid patterns and those of the Tyrannidae also reveal striking similarities and some differences. The patterns of *Muscivora* and *Tyrannus* tend to have the "ovomucoid" and ovalbumin regions close together, as in the Formicariidae but most other tyrannids have these regions more as in the Furnariidae with a marked gap between the "ovomucoid" and ovalbumin sections. One pattern of *Elaenia spectabilis* is similar to that of *Geositta* and several of *Sayornis* are excellent matches for those of *Furnarius* and other furnariids. In most of the available patterns of tyrannids the conalbumin region is faint and smeary. This is in spite of the fact that some specimens (e.g., *Sayornis phoebe*) were undeniably fresh and in the best possible condition. Contrary to this the conalbumins of nearly all formicariids and most furnariids are clear and sharp. The significance of these observations is unknown. Comparisons with other non-oscine groups will be made under those groups.

The pattern of *Geositta* is similar in some respects to that of the wrens. Both show strong pre-albumins in concentrated samples and the remainder of the patterns show other similarities. In gels #S-2207 and #S-2216 (*Geositta* was no longer available) several furnariids and tyrannids were compared with *Troglodytes* and clear differences appear. The wren pattern has a slower component 18 but the conalbumin region is similar to those of the furnariids and tyrannids. In the ovomucoid-ovalbumin region the three groups have a generally similar pattern but the wren components are markedly slower than those of the tyrannids and furnariids. This gel shows that the pre-albumins of the wrens have about the same mobility as the ovalbumins of the tyrannids and furnariids. In all major aspects of their patterns the latter two groups are essentially identical. Thus it seems that the similarities between the patterns of the wrens and those of the New World non-oscines may be superficial. Until these similarities can be tested by other techniques they should remain merely an observation of unknown significance.

FAMILY FORMICARIIDAE, Antbirds. 9/221, fig. 4.

Species examined: *Taraba major*; *Thamnophilus doliatus*, *punctatus*, *caerulescens*; *Dysithamnus puncticeps*; *Myrmotherula axillaris*; *Formicivora grisea*; *Gymnophithys leucaspis*; *Phaenostictus mcleannani*.

Ames (1965) found syringeal evidence to support the alliance of the Furnariidae and Formicariidae while McFarlane (1963) discovered that the sperm morphology of the formicariids apparently differs from that of the furnariids and is similar to that of the tyrannids, cotingids and piprids. McFarlane studied only a few species and the extent of these similarities and differences is therefore unknown. As noted previously the egg-white protein patterns of the formicariids contain both differences and similarities in comparison with those of the furnariids. The available formicariid egg-white specimens show consistently similar electrophoretic patterns which suggests a closely knit group, at least to the extent of the genera represented in this study. They differ from the furnariid patterns in the faster mobility of the conalbumins and in the tendency of the "ovomucoid" to merge with the ovalbumin because it migrates faster. However, dilute patterns of *Thamnophilus* and *Furnarius* are quite similar in the ovalbumin region. It seems reasonable to conclude that these two groups are distinct from one another but related more closely than either is to any Old World group. They are also probably closer to the Tyrannidae than the tyrannids are to any of the Old World groups usually placed in the Tyrannoidea.

FAMILY CONOPOPHAGIDAE, Gnateaters and Ant-pipits. 1/10, fig. 4.

Species examined: *Conopophaga lineata*.

Forbes (1881) believed that *Conopophaga* is closer to the Formicariidae than to the Furnariidae, basing his conclusion on syringeal and other characters. He proposed that Garrod's (1877a) family Conopophagidae be utilized and suggested the Pteroptochidae (= Rhinocryptidae) as its closest relatives. Pycraft (1906) agreed with Forbes although he modified the classification slightly. Heimerdinger and Ames (1967) and Ames et al. (1968) have proposed that *Conopo-*

phaga be included within the Formicariidae and that *Corythopsis* be assigned to the Tyrannidae, thus eliminating the family Conopophagidae.

The egg-white pattern of *Conopophaga* is quite clear and shows an apparently unique pattern. Component 18 is relatively faster than in the Formicariidae, the conalbumin region shows at least six bands, some of which have the same mobility as the conalbumins in the Formicariidae. It is not known whether or not all of these bands are conalbumins in *Conopophaga*. The most anodal may be an "ovomucoid." The ovalbumin region is composed of possibly five bands and I find it impossible to judge whether or not they are similar or different from the same region in the formicariids. Certainly the differences between *Conopophaga* and the formicariids are considerable and whether or not these two groups are each other's closest relatives remains uncertain.

FAMILY RHINOCRYPTIDAE, Tapaculos. 1/26.

Species examined (in disc gel only): *Scytalopus magellanicus*.

The Rhinocryptidae and *Conopophaga* have often been thought to be related. The available egg-white data are poor but the disc gel patterns of *Scytalopus* and *Conopophaga* are unlike. However, until better material can be examined no conclusions can be drawn.

SUPERFAMILY TYRANNOIDEA.

FAMILY COTINGIDAE, Cotingas. 1/90, fig. 4.

Species examined: *Platypsaris aglaiae*.

FAMILY PIPRIDAE, Manakins. 3/59, fig. 4.

Species examined: *Chiroxiphia caudata*, *Manacus manacus*, *Ilicurus militaris*.

FAMILY PHYTOTOMIDAE, Plant-cutters. 2/3, fig. 4.

Species examined: *Phytotoma rutila*, *rara*.

These three groups have often been thought to be related and may be considered together. Garrod (1876b; 1877b) believed the cotingas and manakins to be closely related and that only differences in tarsal scutellation could be used to separate the two groups. Garrod placed the same two families in a single group, the Heteromeri, based upon the development of the femoral artery although *Rupicola* was excluded because in that genus the sciatic artery is the more strongly developed as it is also in *Phytotoma*. Forbes (1880b) followed Garrod in this arrangement. Gadow (1893), who believed that the number and arrangement of syringeal muscles is an unreliable basis for classification, included the manakins and cotingas in the family Tyrannidae. He placed the manakins, the tyrant flycatchers and *Oxyruncus* in the Tyranninae and the cotingas in the Cotinginae. Pycraft (1906, 1907) also kept the Pipridae and Cotingidae adjacent to one another but placed them closer to *Philepitta* and the broadbills than to other New World groups. Pycraft placed *Phytotoma* near the Tyrannidae. Lucas (1895) recommended the establishment of a separate family, the Procnitidae, for the bellbirds based upon palatal characters. Küchler (1936) concluded from an extensive anatomical study that *Phytotoma* belongs in the Cotingidae.

Once again these references indicate the spread of opinion which is encountered. Different persons, using different data and applying different criteria may be expected to arrive at different conclusions. However, there is a core of agreement that the manakins, cotingas and *Phytotoma* are at least members of the same large group and most of the evidence suggests that they are probably closer to one another and to other New World forms than to such Old World groups as the broadbills, *Philepitta*, *Pitta* and *Acanthisitta*.

The egg-white data support this general conclusion. The starch gel patterns of *Platyptaris*, *Chiroxiphia* and *Phytotoma* are similar to one another and to those of the tyrannids and furnariids. Since the dilute patterns of formicariids also show similarities to tyrannids (see p. 38) it follows that these several New World groups have similar patterns.

FAMILY TYRANNIDAE, Tyrant Flycatchers. 45/365, figs. 5, 6

Species examined: *Tyrannus tyrannus*, *melancholicus*; *Empidonomus aurantio-atricristatus*; *Pitangus sulphuratus*, *lictor*; *Sayornis phoebe*, *saya*, *nigricans*; *Myiarchus tyrannulus*, *tuberculifer*; *Contopus virens*, *cinereus*; *Elaenia flavogaster*, *spectabilis*, *albiceps*; *Neoxolmis rufiventris*; *Empidonax traillii*, *difficilis*, *griseus*; *Myiobius barbatus*, *atricaudus*; *Euscarthmornis margaritaceiventer*, *plumbeiceps*; *Myiophobus fasciatus*; *Myiozetetes similis*, *cayanensis*; *Muscivora tyrannus*; *Pipromorpha oleaginea*; *Cnemotriccus fuscatus*; *Xolmis irupero*; *Spizitornis parulus*; *Serpophaga subcristata*; *Mecocerculus leucophrys*; *Platyrrhynchus platyrrhynchus*; *Rhynchocyclus olivaceus*; *Leptopogon amaurocephalus*; *Coryphotriccus parvus*; *Arundinicola leucocephala*; *Pseudocolopteryx flaviventris*; *Machetornis rixosus*; *Knipolegus aterrimus*, *cabanisi*; *Pyrocephalus rubinus*; *Todirostrum cinereum*; *Tachuris rubigatra*.

The boundaries of this family and the relationships within it have been and are a matter of debate and uncertainty. The morphological characters of the group can only be characterized as "variable," for all attempts to find consistent taxonomic characters to define the group have ended in failure. Ridgway (1907) recorded his difficulties and, as others have done, tried to improve the definition of the Tyrannidae by transferring "difficult" genera to other groups.

The history of the classification of the tyrant flycatchers and their relatives abounds in such transfers and attempts to simplify by subdivision. Most classifications have been based upon bill and tarsal characters but von Ihering (1904) produced a classification based upon nest structure, egg color and geographic distribution which had considerable influence upon later workers. Von Berlepsch (1905) followed some of von Ihering's suggestions but relied mainly upon external characters. The opinions of Müller, Garrod and Forbes, who based their classifications upon the syrinx and the development of the thigh artery, have made an alliance among the Tyrannidae, Pittidae and Philepittidae seem acceptable in spite of the opposition of others. For example Gadow (1893) placed the Tyrannidae near the other New World non-oscines and the Old World groups closer to one another. In Newton's *Dictionary* (1896) Gadow emphasized the great variation in the syrinx and noted that a tracheophone syrinx, or indications of it, were found in all of the New World groups with the possible excep-

tion of the Tyrannidae. However, in his earlier work Gadow (1893) concluded that a close relationship exists among the tracheophones and the Tyrannidae. The doubtful value of the development of the thigh artery as an indication of relationships has been noted previously (p. 28).

Pycraft (1906) also supported an alliance between the Tyrannidae and the Pittidae. More recent authors have also placed the "Haploophonae," a mixture of New World and Old World families, in the same superfamily. Mayr and Amadon (1951: 10) note however that the Old World families Pittidae, Xenicidae (Acanthisittidae) and Philepittidae "are very likely more nearly allied to one another than to the Neotropical members of this group." Ames (1965) found the syringeal structure of the Tyrannidae to be variable but he concluded that the Pittidae, Acanthisittidae and Philepittidae are not closely related to the New World non-oscines.

When the tyrannid egg-white patterns are examined against the background of controversy and uncertainty which other approaches have produced one is most impressed by the high degree of similarity which is observed among the patterns of rather diverse genera. There certainly is variation but to my eye the similarities outweigh the differences. In fact, it is my impression that there is no greater variation among the tyrannids than among the furnariids. The differences in some cases are due to variation in sample concentration, in others they are real but not impressively large. The differences among the starch gel patterns of the three species of *Elaenia* are due to quantitative variations in some of the fractions, not to qualitative ones. There is thus a common, reasonably consistent pattern among the species of tyrannids. This is shared with the cotingids, piprids, *Phytotoma* and furnariids. The formicariids seem to differ from these other groups in some aspects of the pattern but dilute specimens of *Thamnophilus*, *Furnarius* and *Muscivora* are remarkably similar to one another in the ovalbumin region.

Comparisons among the tyrannid patterns, those of other New World groups and those of *Psarisomus*, *Smithornis*, *Acanthisitta* and *Pitta* reveal that the New World families have patterns more similar to those of one another than to those of any of the Old World groups.

FAMILY PITTIDAE, Pittas. 2/23, fig. 7.

Species examined: *Pitta angolensis*, *erythrogaster*.

FAMILY ACANTHISITTIDAE (XENICIDAE), New Zealand Wrens. 1/4, fig. 7.

Species examined: *Acanthisitta chloris*.

FAMILY PHILEPITTIDAE, Asities. 0/4.

These three groups, although probably not closely related, are all Old World in distribution. The genus *Pitta* occurs mainly in southeast Asia and Australia. There is one species in Africa. The pittas are morphologically distinctive and have been placed in the Tyrannoidea only because they have a tracheo-bronchial (haploophone) syrinx. Ames (1965) has found sufficient evidence of syringeal

differences between pittas and the New World haploophone groups to indicate that the alliance of the Pittidae with the New World tyrannoids is based upon superficial resemblances and that the two groups are probably not related to the degree suggested by inclusion in the same superfamily.

The egg-white pattern of *Pitta* supports Ames' conclusion. The pattern of *Pitta* in starch gel differs in several major respects from those of the New World suboscines. If the closest relatives of *Pitta* are not to be found among the suboscines, it must be assumed that they are oscines. Comparisons between *Pitta* and various oscine groups reveal several with similar patterns but until more definite evidence is found it seems best to leave this question open.

Essentially the same comments may be made concerning the New Zealand Wrens. Forbes (1882) allied the Acanthisittidae to the Pipridae, Tyrannidae, Pittidae and Philepittidae because they share the haploophone syrinx. Pycraft (1905a) disagreed with Forbes and, although he recognized that the syringes differ, placed the New Zealand Wrens closer to the Furnariidae because they have similar palatal characters and schizorhinal nares. Pycraft suggested that the Acanthisittidae should occupy a place between the Pipridae and the tracheophones and (1906) placed the family Xenicidae (Acanthisittidae) in his sub-order Tracheophonae. Oliver (1945) commented briefly upon certain skeletal characters in *Acanthisitta* and noted that the vomer of *Pitta* is unlike that of *Acanthisitta* although the maxillo-palatines are entire in both genera.

These various characters are of doubtful value as indicators of relationships at the higher levels. Bock (1960) has discredited the palatine process of the pre-maxilla as a taxonomic character and the shape of the nares surely reflects an adaptive response at least as much as it indicates relationship. Ames (1965) was unable to find convincing syringeal evidence to ally the New Zealand Wrens to the New World Tyrannoidea.

The available starch gel egg-white pattern of *Acanthisitta chloris* is excellent and it differs in many respects from those of the New World non-oscine groups. I therefore agree with Ames that the nearest relatives of the New Zealand Wrens are not the Tyrannoidea. Again it seems reasonable to assume that the true relatives should be sought among the oscines but I am reluctant to call attention to any resemblances until additional evidence is available. The egg-white patterns are useful in suggesting lack of relationship and in demonstrating the cohesion of a closely related group but they cannot, alone, provide a firm basis for suggesting an alliance between groups for which there is no other evidence of relationship.

The presently available evidence, from all sources, suggests: 1) that it is highly probable that the New World groups of non-oscine passerines are more closely related to one another than any one of them is to any of the Old World non-oscine groups, and 2) that it is improbable that the Eurylaimidae, Acanthisittidae and Pittidae are closely related to one another.

Before translating these probabilities into proposals for changes in the presently accepted classification they should be tested by additional techniques.

SUBORDER MENURAE.

FAMILY MENURIDAE, Lyrebirds. 1/2, fig. 7.

Species examined: *Menura novaehollandiae*.

The relationships of the lyrebirds are obscure and, except for the Australian genus *Atrichornis*, no reasonable relatives have been suggested. The available egg-white patterns of *Menura* are excellent but they do not offer any obvious clues to possible relatives.

THE OSCINE PASSERINES

(SUBORDER PASSERES)

HISTORICAL REVIEW OF THE CLASSIFICATION OF THE OSCINES

The suborder Passeres is composed of diacromyodian passerines with more than three pairs of intrinsic syringeal muscles. This diagnosis defines a group of approximately 4000 species, thus by far the largest suborder of birds. The subdivision of the suborder into families has been difficult because few groups which could rank as families are well defined. Even more elusive, as Beecher (1953: 275) has noted, has been evidence for showing the degrees of relationship among the families.

Some indication of the range of opinion concerning these problems is gained by noting the number of families used in recent years by different systematists. Stresemann (1934) arranged the group in 49 families, Mayr and Amadon (1951) in 36, Mayr and Greenway (1956) in 40, Amadon (1957) in 42, Delacour and Vaurie (1957) in 39 and Wetmore (1960) in 54. The sequence of families to be followed in a linear list that would express an evolutionary lineage from "primitive" to "advanced" has also produced disagreement (Mayr and Greenway, 1956; Wetmore, 1957; Mayr, 1958; Storer, 1959).

One of the characters that have been used as a basis upon which to subdivide the Passeres is the number of primaries. To determine the number of primaries would seem to require nothing more than the counting of a series of discrete structures but the history of this problem provides us with examples of several of the difficulties which beset avian systematists.

Nitzsch (1840) was the first to note that passerines usually have ten primaries but that the outermost is always shorter than the others and is apparently absent in some species. Wallace (1874) counted the number of primaries in many species and found certain correlations between the number of primaries and other characters. For example, he noted that those passerine birds with ten well-developed primaries also have an "imperfect singing apparatus", i.e., the non-oscines. All others have nine primaries or a very small tenth. Wallace proposed a subdivision of the Passeres, as follows [using Wetmore's (1960) family units and sequence]:

- 1) Ten primaries, outermost reduced in size but present. This condition is found in the Dicruridae, Oriolidae, Corvidae, Paradisidae, Paridae, Certhiidae, Timaliidae, Campephagidae, Pycnonotidae, Cinclidae, Troglodytidae, Turdidae, Sylviidae, Muscicapidae, Laniidae, Meliphagidae, Nectariniidae and Vireonidae.
- 2) Ten primaries, outer rudimentary. Alaudidae, Artamidae, Sturnidae and Ploceidae.
- 3) Nine primaries, outer well-developed. Hirundinidae, Motacillidae, Bombycillidae, Dicaeidae, Coerebidae, Drepanididae, Parulidae, Icteridae, Thraupidae and Fringillidae.

Wallace noted that of 13 families confined to the New World, 12 have a well-developed outer primary, either number nine or ten. In the Old World out of 29 families, 22 have a rudimentary outer primary. The seven Old World families with well-developed outer primaries are small groups of relatively uniform structure.

Sclater (1880, 1881) rightly criticized Wallace's arrangement because it "separates some very nearly allied forms far too widely" and because it did not take into account the variation in the development of the outer primary within the Alaudidae and the genus *Vireo*. However, Sclater also wrongly criticized Wallace because his scheme placed the Sturnidae and Icteridae in different groups, an arrangement that Sclater deplored because there "cannot be a doubt as to the intimate connexion [*sic*] of the two last-named families."

Jeffries (1881), strongly influenced by Darwinian concepts, tried to reconstruct the history of changes in the avian wing. Jeffries credited Baird (1864: 160) with being the first to show that in the "nine-primaried *Oscines*" there are two "little feathers" placed at the end of the wing, which Baird judged to represent the outermost (tenth) primary and its covert. In ten-primaried birds there is but one little feather which Baird considered to be a covert. Jeffries also reviewed the opinions of Coues and Batchelder concerning the problem and then reported upon his own studies of young oscines and other birds in which the developing feather papillae could be seen. Jeffries concluded that the number of functional primaries in the oscines is either nine or ten and that in the nine-primaried species the outermost primary (the tenth) and its covert are very small. The rest of the oscines have ten functional primaries and nine coverts. Jeffries noted (p. 163) that "the number of primaries does not hold constant for the larger groups of birds, but . . . the higher birds of the various groups show a tendency towards the reduction in the number of primaries. So the reduced number of primaries and coverts would seem to point to high development, but not to be of use in dividing the major groups." Jeffries also suggested that "The rule according to which the primaries and coverts abort . . . makes it possible to decide whether a 'little feather' be a primary or a covert. The law is simply that the most distal one aborts first, hence a covert before its primary. Hence when one 'little feather' is found we can tell if it be a covert, as in the *Tyrannidae*, or a primary, as in the Kingfishers, by seeing what the next developed feather is,—in the first case a primary, in the last a covert. When there are two little feathers one is a primary and the other a covert, the covert being uppermost."

Jeffries paper was unknown to Wray (1887) who took as his starting point a rather unsatisfactory account by Sundevall (1843) which had been translated into English in 1886. Wray also found the "little feather," called it the "remicle" and, like Jeffries, interpreted it as the vestige of a functional primary. He noted (p. 344) that "its relations, described in detail later, show that it is as much a primary as the so-called 'spurious tenth' of many Passerines." Gadow (1888) and Degen (1894) agreed with Wray (and Jeffries) that the reduction in the number of primaries takes place at the terminal end of the wing.

In 1898 Butler and Butler, apparently unaware of the papers by Jeffries, Wray, Gadow and Degen, independently discovered the "little feather" in several

groups of passerines. They examined some nestlings and advanced embryos, as well as adult specimens and concluded that a tenth primary is actually present, but "concealed within its coverts" in the Fringillidae, Motacillidae, Hirundinidae and Icteridae.

Miller (1924) reviewed several aspects of pterylosis and concluded that the passerines have ten primaries with the outermost vestigial in the "9-primaried" groups. Stegmann (1962) followed Jeffries and Gadow in believing that any reduction in the number of primaries begins with the outermost. Stegmann further suggested that the remaining primaries may then migrate distally, thus accounting for the present arrangements found in different groups in regard to the number of primaries on the metacarpals and digits.

Stresemann (1963) questioned the assumption, which began with Jeffries (1881), that the remicle is homologous to a primary. Instead Stresemann proposed that the remicle is the vestige of a covert attached to the end of the second phalanx of digit II which covered the clawed third phalanx. Following the atrophy of the claw and its phalanx the remicle persisted in some groups but tended to degenerate.

But this is not yet the final answer. In November 1967, I wrote to Prof. Stresemann and asked him to clarify for me the relationship between the small feathers which the Butlers (1898) had described and the remicle of Wray and others. In his reply, dated December 4, 1967, Prof. Stresemann stated that the outermost feather to which Butler and Butler referred as "the first primary" is "the abortive pr. 10 and *not* the remicle. The remicle is found in some species of Passerines, mostly belonging to the Corvidae and Laniidae, but always absent in Ploceidae, Fringillidae, Estrildidae, etc." Stresemann went on to say that, "After studying the remicle problem more thoroughly [than] I had done in 1963, I now consider the remicle a *primary*, which has been . . . minute from the start. Being fixed at the distal end of phalanx 3 (or 2) of the second digit it was doomed to remain very short, and hidden under the upper greater covert of pr. 10. It became vestigial or completely absent in the majority of groups. See the list (a very reliable one!) in . . . Miller (1924: 317)."

In a further letter on this subject, dated January 8, 1968, Prof. Stresemann stated that he considered the remicle to be the homolog of primary No. 11 but only in birds with six metacarpal primaries, not in those with seven metacarpal primaries, such as some storks, the flamingos and the grebes, or those with five such as the Indicatoridae. Prof. Stresemann noted that the remicle meets the definition of a primary by being fixed to the skeleton and by having a corresponding greater under wing covert.

The remicle (*vide* Stresemann, *in litt.*) is fairly well developed in the genus *Corvus* and in some other Corvidae but minute or lacking in others. It is also present in some species of the Laniidae, in the genus *Picathartes* and in a few species in other groups of the Passeriformes. Prof. Stresemann notes that most probably the remicle is an ancestral little feather which, at present, is in various stages of reduction and has altogether disappeared in many groups and that "It's taxonomic value is very limited!"

In two subsequent papers Stresemann and Stephan (1968a, b) have discussed the origin and significance of the remicle.

Another aspect of this problem concerns the adaptive significance and taxonomic value of the shape of the wing. Averill (1925) was able to demonstrate that wing shape, development of the outer primary, and length of the migratory flight tend to be correlated. His conclusions may be summarized as follows:

- 1) The development of the outer primary varies inversely as the wing varies in length.
- 2) In the Vireonidae there is a decrease in the relative size of the outer primary with a northerly extension of breeding range and consequent increase of the length of the migratory flight.
- 3) The Turdidae show a similar trend.
- 4) No North American ten-primaried oscine makes a long migration unless the outer primary is minute or apparently lacking and no member of a tropical or subtropical group has become a migrant to North America without evolving an elongated wing and a reduced outer primary.

Averill's observations have been supported by Kipp (1942, 1955), Meinertzhagen (1951), Hamilton (1958), Dorst (1962), Stegmann (1962) and Parker and Harrison (1963). It seems clear that the shape of the wing is therefore unlikely to be a reliable clue to taxonomic relationships.

The complexity of the problem of the number of primaries and their adaptive and taxonomic significance is obvious. There are some examples of taxonomic correlation, notably the "nine-primaried oscines" (= Fringillidae of this paper). Among the New World representatives of this group there are species which are highly migratory, others which are sedentary. Although the *shape* of the wing tends to vary in correlation with migratory behavior, all members of this large assemblage have but nine primaries. However, the emberizine genus *Urocynchramus* of Asia has a relatively long tenth primary (Mayr and Amadon, 1951). In addition there is no convincing evidence that other nine-primaried passerines (Hirundinidae, Motacillidae, Bombycillidae, Zosteropidae, Dicaeidae) are related to the Fringillidae (as defined herein). Neither is there proof that some ten-primaried passerine families are not more closely related to some nine-primaried groups than to other ten-primaried groups. In short, although some degree of correlation can be demonstrated between the number of primaries and certain generally accepted natural groups, it is not valid to assume that the number of primaries is a completely reliable character for the delineation of passerine families.

The counts of secondaries by Stephan (1966) showed that many species have more than the usual nine. There are 13 secondaries in *Menura*, in some bower birds and some birds of paradise. Having more than nine is characteristic of the larks and of all of those groups which Mayr and Amadon (1951) called "Shrikes and Allies," "Waxwings and Wood Swallows" and "Crows and Australian Crow-like Birds." Because *Picathartes* has 10 or 11 secondaries Stephan suggests that it belongs near the Corvidae. Other groups are also considered to be misplaced on a similar basis. The Oriolidae, for example, which have 10 or 11 secondaries, are placed by Stephan closer to the "Shrikes and Allies" than to the Ploceidae and Sturnidae as in Wetmore's sequence (1960).

Whether or not the number of secondaries is a reliable index to taxonomic relationships remains to be proved. In view of the possible functional significance of variation in the number of secondaries it seems reasonable to be skeptical about Stephan's taxonomic conclusions but his data should be explained, not ignored. In at least one case, that of *Picathartes*, the egg-white evidence is in conflict with Stephan's suggestions.

In two long and involved papers Parker (1875, 1878) examined the palate and the "face" of the aegithognathous birds, including many passerines. Many of Parker's statements make little taxonomic sense, others reflect keen insight and critical evaluation. For example Parker (1878: 285-288) agreed with Newton that *Panurus* is not a true parid but then proceeded to put both *Suthora* and *Cyclorhis* (= *Cyclarhis*) also in the Paridae. Parker was apparently really concerned with morphological patterns, which may or may not indicate genetic relationships. He had limited material which he viewed through a haze of doubtful theory and he seldom thought in functional terms. On the other hand his more strictly descriptive studies of avian morphology (e.g., 1872) were praised by Newton (1893: 79-81) and by Bock (1960).

Shufeldt (1889a) considered the evidence of relationships among the North American Passeres as indicated by the skeleton. His usual rather casual narrative, replete with observations and suggestions, concludes with the proposal that the Corvidae should be placed "at the head of the Passeres," i.e. at the end of a linear list. Shufeldt's list would thus show the following sequence, using Wetmore's (1960) family names: Tyrannidae, Laniidae, Bombycillidae, Hirundinidae, Alaudidae, Certhiidae, Vireonidae, Motacillidae, Sylviidae, Coerebidae, Parulidae, Cinclidae, Troglodytidae, Turdidae, Paridae, Thraupidae, Fringillidae, Icteridae, Sturnidae, Corvidae.

Shufeldt attempted to make this sequence reflect his interpretations of osteological characters as indicators of natural relationships. Although he qualified the assignments of positions in many cases it is instructive to note certain points that suggest that Shufeldt's years of study of the avian skeleton did not provide him with clear evidence of relationships. The most striking example is that the Parulidae and Coerebidae are placed so far from the Thraupidae, Fringillidae and Icteridae, for it is doubtful that any avian systematist today questions the close affinities of these groups.

In his famous article on ornithology in the ninth edition of the Encyclopedia Britannica, Newton (1884) reviewed the history of avian classification and provided critical and often sharply worded comments upon the various schemes that had been proposed. This article was reproduced, virtually unchanged, as the first 97 pages of the Introduction to Newton's *Dictionary* (1896). Newton (1896: 115) concluded that the work of Garrod, Forbes and Gadow had been of great service in determining passerine relationships but that the oscines, with few exceptions, could not be subdivided into definable groups because most of the possible subdivisions gradually merge with others. He did however, conclude that the Corvidae should occupy the top position in a linear list because of their larger brain capacity and because the immature plumage is like that of the adult, a condition which Newton considered to be superior to that in which the immature plumage differs from that of the adult or, in sexually dimorphic species,

is like that of the adult female. Newton's arguments (p. 117) on this point are obscure and confused. The fact that the immature plumage could be the result of adaptation and not importantly indicative of "ancestral characters" apparently escaped him.

Oates (1889) also attempted to classify the Passeres on the basis of the pattern of the juvenal plumage. His groupings were as follows, using Wetmore's (1960) family names:

- 1) Plumage of nestling like that of adult female, but paler: Corvidae, Timaliidae, Sittidae, Dicuridae, Certhiidae, Regulidae.
- 2) Nestling like adult female, but brighter: Sylviidae.
- 3) Nestling cross-barred: Laniidae.
- 4) Nestling streaked: Oriolidae, Sturnidae.
- 5) Nestling mottled or squamated: Muscicapidae, Turdidae.

It seems obvious that the color pattern of the juvenal plumage is simply adaptive and that similar patterns do not necessarily indicate genetic relationships. The frequent occurrence of similar juvenal and adult female plumages is probably due to what may be called "intraspecific convergence," i.e. both are adapted for concealment from predators or to avoid the kinds of interactions with which the adult males of the species must cope. The possession of a female-type plumage probably permits the young birds in juvenal plumage to move about without having to respond constantly to the challenges of territory-holding adult males. In those species in which this problem is not acute other patterns evolve in response to other sources of selection.

One of the most persistent beliefs concerning the taxonomic value of juvenal plumage patterns involves the spotted young of some thrushes and some muscicapids. This spotting is one of the characters usually cited as indicating a relationship between the two groups. However, not all species in these groups have spotted juvenal plumages and the Sylviidae, which are probably closer to the Muscicapidae than are the Turdidae, do not have spotted young.

Sharpe (1891) presented a diagram to show the supposed relationships of the families of oscines. This "map" places the Fringillidae, Icteridae, Coerebidae and Thraupidae in the same group but the Parulidae are placed outside and are indicated as allied to the Motacillidae via *Seiurus* and to the Certhiidae via *Mniotilta*. The Alaudidae are indicated as allied to the Fringillidae by a connection between *Otocorys* (= *Eremophila*) and *Plectrophenax*. Similar alliances between other convergently similar genera indicate that Sharpe had not perceived the fallacies in this approach.

Although Fürbringer (1888), Gadow (1893), and Beddard (1898) considered the non-passerines in detail they gave little attention to the problems of passerine classification below the suborders. Stresemann (1934) devoted 107 pages to the non-passerines and six pages to the non-oscines but only a little over two pages to a bare listing of the oscine families and their geographic distributions.

As Bock (1960: 362) has noted such unbalanced treatments simply reflect the conviction that the oscines are morphologically uniform and that there is

little hope of untangling relationships within the group. To a degree this is true, but Bock (1960) has cited some 25 papers which contain evidence that the passerines are not absolutely uniform in their internal anatomy. At the same time Bock proved that one character, the palatine process of the premaxilla, "has *little or no* value in showing relationships between families of passerine birds." In a later study of the pneumatic fossa of the humerus Bock (1962b) concluded that it was not possible to determine "the taxonomic value of the pneumatic fossa at this time" and recommended that it "be used with great caution in passerine systematics until more has been learned about its function and evolution."

Heimerdinger (1964) and Ames, Heimerdinger and Warter (1968) have discussed passerine pterylosis as a basis for classification. They report (1968: 22) "that pterylosis is a remarkably constant and conservative anatomical character in passerines." Individual variation is not significant and most of the families, superfamilies and suborders can be characterized by differences in the patterns of feather rows or in their presence or absence. A few groups, including the Corvidae, Sturnidae, Nectariniidae, Vireonidae and Ploceidae are noted by Heimerdinger (1964) as relatively variable in their patterns of pterylosis. Bock (1962a) also noted the variation in the dorsal feather tracts of the Corvidae. On other grounds, for example the wing musculature (Hudson and Lanzillotti, 1955), the corvids seem to be a closely-knit group.

From his study of the syrinx Ames (1965) concluded that the Passeres are closely related to one another and form a monophyletic unit. Ames did not attempt to distinguish families within the Passeres.

Beecher's (1953) study of the jaw muscles of the oscines led him to conclude that the Sylviidae are probably close to the ancestral oscines. Beecher's conclusions have not been generally accepted (see Bock, 1960: 400-402) but he did present a body of data which must be considered in relation to other sources of evidence about passerine relationships. His conclusions will be considered in more detail in the family accounts which follow.

A few other papers have considered the relationships of some of the families of Passeres. Jollie (1958) responded to the papers by Beecher (1953) and Tordoff (1954a, b) with some comments on the passerine skull. He concluded that the form of the prefrontal bone is of taxonomic value in the oscines and that the larger species, for example the crows, are the more primitive while the smaller species are the more specialized. Stallcup (1961) used serology for a comparison of the saline-soluble tissue proteins of 15 families of North American passerines. His antigenic material was an extract of muscle tissue which could be expected to contain a large number of different proteins, including those of the blood as well as those of muscle tissue, many enzymes, etc. The antisera were prepared in the standard way in rabbits and the results of the precipitin tests were determined with the Libby "Photronreflectometer", which measures the turbidity of a solution. This procedure has frequently been criticized and Stallcup discusses some of these problems. His taxonomic conclusions agree with other data in some cases but disagree in others. They will be noted in the family accounts which follow. Andrew (1961) compared certain display movements in many groups of passerines and provided taxonomic comments on a number of problems. Again,

these conclusions show varying degrees of concordance with data from other sources and will be noted in the family accounts.

Pocock (1966) has compared several families of Passeres on the basis of the presence or absence of a certain process ("Process D") on the carpometacarpus. The process is absent in the Laniidae, Prionopidae, Dicruridae, Corvidae and some genera (*Batis*, *Terpsiphone*) of the Muscicapidae. It is present in many other families and in other genera of Muscicapidae. Pocock also examined certain foramina in the skull and concluded (p. 94) that "the Passeridae are less closely related to *Plocepasser* and the rest of the Ploceidae than usually believed and hence deserve family rank." However, Karl Tolonen (see p. 92) has examined additional species and his observations cast doubt on the taxonomic value of the foramina studied by Pocock.

The manner in which a passerine bird scratches its head, either "directly" (under the wing) or "indirectly" (over the wing) has been examined as a taxonomic character by Simmons (1957, 1961) and reviewed recently by Ficken and Ficken (1966). Berger (1966) has added further observations. The types of variation which have been found and the lack of concordance with certain other characters make it essentially impossible to assess the taxonomic value of this behavior pattern. Other behavioral characters which have been used in taxonomy are reviewed by Ficken and Ficken (1966) and Cullen (1959).

We are thus presented with a considerable array of evidence in a variety of forms and derived from a variety of materials using many different methods. In most studies only part of the oscine families have been examined. The data on egg-white patterns to be presented in the following section suffer from these same disabilities. Various "suggestions" will be made, but I will avoid the use of the words "proof" or "proved." In many cases not even tentative suggestions can be offered, in others several kinds of data are concordant and one seems to be justified in believing that evidence of genetic relatedness is demonstrable.

THE EGG-WHITE PROTEIN DATA

FAMILY ALAUDIDAE, Larks. 12/75, fig. 7.

Species examined: *Alauda arvensis*; *Eremophila alpestris*; *Lullula arborea*; *Galerida cristata*, *theklae*, *malabarica*; *Calandrella cinerea*; *Melanocorypha calandra*; *Eremopteryx leucopareia*; *Mirafra africanoides*, *cantillans*; *Certhilauda albescens*.

The larks have usually been considered a well-marked group with no close relatives since Keyserling and Blasius (1839) noted the latiplantar tarsus. This character and the lack of an ossified pessulus in the syrinx distinguish the larks from other oscines.

Some classifications have placed the larks near the emberizine or ploceine finches, at least in part because some larks are finch-billed and because of the reduction of the tenth primary to a rudiment or to the nine-primaried condition in some genera. Berlioz (1950) has advocated an arrangement that allies the Alaudidae and the Motacillidae to one another and to the Fringillidae and Ploceidae. Mayr and Greenway (1956) rejected an alliance between larks and

finches on the basis that the differences are large and that the heavy bill in some seed-eating genera of larks, and the reduction in the number of primaries, cannot be considered evidence for relationship to the finches.

Beecher (1953: 314) interpreted his jaw muscle data as indicating an origin for the larks "from the Cisticolinae close to the pipits, monarchs, and parrot-bills." This conclusion has been challenged by Mayr (1955). Beecher (1953: 315) considered the tarsal scutellation in the larks to be simply a "unique specialization" not to be accorded much weight.

The Type A starch gel electrophoretic patterns of the egg-white proteins of the various species of larks are essentially identical. The patterns of several species indicate that a pre-albumin is present. The lark pattern is like that of the swallows in most respects and the differences are of uncertain significance. The lark pattern resembles that of the emberizines and other "higher" nine-primaried oscines in the slow mobility of component 18, in the albumin region and in the presence of a pre-albumin. The conalbumins in the larks are relatively slower than in the emberizines thus producing a larger gap between the conalbumins and the albumins. This gap is further increased because the albumins in the larks move faster than in the emberizines. The resulting patterns of the two groups thus resemble one another in many respects but they also differ. The similarities do not prove a relationship and the differences do not rule it out.

The lark pattern is more like those of the Sylviidae and Motacillidae than of the Turdidae. It is unlike those of the Sturnidae, Corvidae, Ploceidae and various other Type B groups. In summary, although the lark egg-white patterns do not provide proof of relationship to any one group they do indicate that the sylviids, motacillids, swallows and even the emberizines could be related but that the ploceids probably are not.

FAMILY HIRUNDINIDAE, Swallows. 23/75, figs. 7, 8.

Species examined: *Tachycineta bicolor*; *Progne chalybea*; *Stelgidopteryx ruficollis*; *Riparia paludicola*, *riparia*; *Hirundo rustica*, *tahitica*, *albigularis*, *aethiopica*, *smithii*; *Cecropis cucullata*, *abyssinica*, *semirufa*, *senegalensis*, *aurica*, *striolata*; *Petrochelidon rufigula*, *ariel*, *preussi*, *spilodera*, *pyrrhonota*, *fulva*; *Delichon urbica*.

Like the larks, the swallows seem to be a distinctive, monophyletic group of uncertain affinities. Beecher (1953) suggested a derivation from the Muscicapidae with affinities to the Sturnidae, Sylviidae and Turdidae.

The Type A starch gel patterns of the swallows resemble those of several other groups, including the Sylviidae and Muscicapidae. They are less like those of the thrushes and starlings, although some patterns of the swallows do suggest the presence of a visible "ovomucoid" fraction as in thrushes, starlings and other Type B groups.

The closest living relatives of the swallows are probably some other group of oscines but the evidence is conflicting and, so far, unconvincing. It seems logical to seek these relatives among the insect eaters. However, one should not forget that among the close relatives of the emberizines and thraupines are the insect-eating parulines.

FAMILY DICRURIDAE, Drongos. 4/20, figs. 8, 9.

Species examined: *Dicrurus adsimilis*, *aeneus*, *leucophaeus*, *ludwigii*.

Mayr and Vaurie (1948) have published a study of evolution within this family and Vaurie (1949) has reviewed the relationships of the group to other passerines. The older literature cited by Vaurie contains various suggestions based upon plumage characters, habits, egg coloration, etc. but no conclusive evidence of relationships. Mayr and Amadon (1951: 30) placed the drongos close to the Oriolidae, although they noted that "it may be that both families are better placed in the vicinity of the Campephagidae." Beecher (1953) erected a new family, Monarchidae, to contain the monarchs (*Monarcha*, *Terpsiphone*, *Rhipidura*, etc.), the whistlers (*Pachycephala*), the drongos and the vireos. Bock (1962b) found that the drongos have a single humeral fossa as do the Oriolidae and several other families. The double condition is developing, but incomplete, in the Muscicapidae, vireos, bulbuls and Campephagidae. Pocock (1966) found that the drongos, shrikes, crows, Prionopidae and the muscicapid genera *Batis* and *Terpsiphone* lack "Process D" on the carpometacarpus while many other passerine groups have it.

The Type B starch gel pattern of the egg-white proteins of *Dicrurus* resembles those of *Sturnus*, *Turdus* and *Pycnonotus* more closely than that of *Campephaga*. The *Dicrurus* pattern is not convincingly similar to those of *Muscicapa* or *Vireo*. The pattern of *Dicrurus* does not match those of *Oriolus*, *Rhipidura*, and *Pachycephala* as well as it does those of *Sturnus* and *Pycnonotus*. The patterns of the Corvidae and Laniidae differ from that of *Dicrurus* in several respects. The drongo pattern is also unlike that of the Paradiseidae, an alliance suggested by Hartert (1919). Thus, of the many suggestions, the egg-white data seem best to support a relationship between drongos and bulbuls but this, too, is only a suggestion that remains to be proved. The similarity between the patterns of *Dicrurus* and *Turdus* is of uncertain significance. Both are Type B patterns, due to the presence of an "ovomuroid" fraction, but there seems to be no other evidence to suggest an alliance between them.

FAMILY ORIOLIDAE, Old World Orioles. 3/35, fig. 9.

Species examined: *Oriolus oriolus*, *sagittatus*; *Irena puella*.

Mayr and Amadon (1951) tentatively placed the orioles and drongos near one another. Beecher (1953) interpreted his jaw muscle data as indicating that the orioles were derived from the bulbuls and related also to the Corvidae. Amadon (1956: 9) mentions the Oriolidae as one of several families sharing "similar morphological attributes" with the Sturnidae.

The Type B egg-white patterns of *Oriolus*, *Dicrurus* and *Pycnonotus* are generally similar to one another and also to several other genera including *Sturnus*. Resemblances to the Corvidae are not impressive. Egg-white specimens from *Corvus* and *Oriolus* have been compared side by side in starch gel and the mobilities of the ovalbumins prove to be quite different.

It seems possible that *Oriolus* is related to *Dicrurus*, *Pycnonotus* and possibly *Sturnus* but it also seems prudent to avoid further speculation. The oriolids are distinctive as a group but their affinities are certainly not completely clear.

The fairy bluebirds, *Irena*, have usually been placed in or near the bulbuls, drongos, orioles or cuckoo-shrikes. Oberholser (1917) reviewed some of the previous opinions and proposed that *Irena* be removed from the Pycnonotidae and made the type of a new family, Irenidae. Oberholser noted that *Irena* had been placed with the bulbuls because it has conspicuous nuchal "hairs" but that *Irena* also resembles the drongos in having metallic plumage and heavily plumed nostrils. However, since *Irena* has 12 rectrices, rather than 10 as in drongos, Oberholser concluded that the fairy bluebirds could not be members of the Dicruridae.

Delacour (1946a) included *Irena* with *Aegithina* and *Chloropsis* in the Aegithinidae but Berlioz (1950) maintained the family Irenidae next to the Oriolidae. Berlioz noted that *Irena* shares certain characters with the drongos, orioles, bulbuls and thrushes. Beecher (1953) made the Irenini a tribe of the Pycnonotinae in the Sylviidae.

Wetmore (1960) separated *Aegithina* and *Chloropsis* from the bulbuls on skull characters and set up the family Chloropseidae to accommodate these two genera. He placed *Irena* in the subfamily Ireninae of the Oriolidae because of osteological similarities between *Irena* and *Oriolus*.

The egg-white pattern of *Irena puella* matches well enough those of *Pycnonotus*, *Oriolus* and *Dicrurus* to support its allocation to this assemblage but the available pattern of *Irena* is not good enough to provide a basis for speculation about which of these groups is closest to *Irena*. The pattern of *Irena* is not a good match for that of *Turdus*.

FAMILY CORVIDAE, Crows, Jays, etc. 20/100, figs. 9, 10.

Species examined: *Corvus monedula*, *frugilegus*, *corone*, *corax*, *bennetti*, *brachyrhynchos*, *cryptoleucus*, *albus*, *cornix*, *coronoides*; *Cyanocitta cristata*, *stelleri*; *Aphelocoma coerulescens*; *Pyrrhocorax pyrrhocorax*; *Cyanopica cyana*; *Pica pica*; *Perisoreus canadensis*; *Cyanocorax yncas*; *Psilorhinus morio*; *Garrulus glandarius*.

As Amadon (1944) noted there seems to be no reason to doubt that the family Corvidae is a monophyletic group of closely related genera. Studies such as those of Ashley (1941) on the humerus and Hudson and Lanzillotti (1955) on the wing muscles support this view. The egg-white protein patterns are also impressively uniform, although the jays and magpies do show small differences from *Corvus*. Material from the more aberrant genera has not been available.

The pterylography of the Corvidae, however, proves to be highly variable (Lowe, 1938; Bock, 1962a; Heimerdinger, 1964). Bock found "that the variation in the dorsal feather tract of the Corvidae is almost as great as the known variation of this feature in the entire order of perching birds." Bock concluded that the assumption that the dorsal feather tract does not vary within a closely related group of genera is untrue.

The question of the relationships of the Corvidae to other passerine groups has produced a remarkable amount of speculation and debate. Some of the suggested alliances are clearly based upon convergent similarities and may be disregarded. For example, Shufeldt (1888) proposed that similarities between the skulls of *Sturnella* and *Cyanocephalus* indicate that the Icteridae and Cor-

vidae are related. More complex is the question of relationship between the Corvidae and the several families endemic to the Australian region that resemble the corvids in size and general appearance. These are the Cracticidae, Grallinidae, Ptilonorynchidae, Paradiseidae and Callaeidae. Other groups often considered to be related to the Corvidae are the Oriolidae, Dicruridae, Prionopidae, Van-gidae, Sturnidae, *Picathartes*, Laniidae and Paridae.

Leach (1914) sought to clarify the relationships between the Corvidae and the Cracticidae by a study of the myology, osteology and pterylosis of *Strepera*, *Gymnorhina* and *Cracticus* which he compared with Shufeldt's (1890) description of the raven. Leach concluded that the three Australian genera are closely related to one another and that there is no evidence of relationship between them and *Corvus*. Shufeldt (1923) later decided that *Grallina* is not related to the Corvidae but that *Corcorax* may be. He also thought that *Struthidea* is not related to *Corcorax* nor to the corvids. Mayr (1931) concluded from a study of the syrinx that the Cracticidae are related to the Corvidae.

The relationships of the Corvidae to other passerine groups were discussed by Amadon (1944) who advocated the establishment of an enlarged family to include the typical corvids, the birds of paradise, Old World orioles, drongos and cracticids. Amadon thought that the Prionopidae probably should not be included and that the Callaeidae, *Struthidea* and *Corcorax* probably should be. *Picathartes* was considered by Amadon to be doubtfully a corvid, not a starling, and possibly a "very aberrant offshoot of the thrush-babbler assemblage" (p. 3). In 1950 Amadon concluded that *Corcorax* and *Struthidea* are not related to the Corvidae and in 1951 he considered the relationships of the corvids to the Cracticidae and the other Australian groups to be "a moot question." Mayr and Amadon (1951, p. 31) placed the Corvidae near the "Australian corvid-like families" (Grallinidae, Callaeidae, Cracticidae, Ptilonorynchidae, Paradiseidae) but pointed out that they "may well be of independent evolution." In a later classification Amadon (1957) kept these various groups as separate families but in the same "broad level of evolution" as the Corvidae.

Many authors have considered the possibility of a relationship between the Corvidae and the Paradiseidae. Most of the older classifications and many of the recent ones (e.g., Mayr and Greenway, 1956; Delacour and Vaurie, 1957; Amadon, 1957; Mayr and Greenway, 1962) place the Corvidae and Paradiseidae either as adjacent families or near to one another. Stonor (1938) found the pterylosis of the birds of paradise to be similar to that of the Corvidae but Berger (1956b: 444), although confirming Stonor's description of the pterylosis, concluded that the "patterns of the dorsal feather tracts do not seem to indicate close relationship of the Corvidae with the Paradiseidae." Berger also found myological differences between the two groups and little in the skeletons to indicate relationship except in the broadest sense. He concluded that the two groups are not closely related.

Beecher (1953) derived the corvids from the bulbuls and thought them to be close to the Oriolidae but Jollie (1958) noted that Beecher's drawings of the jaw muscles of the Corvidae were like those of the shrikes as well as like those of *Oriolus*. Fiedler (1951) had earlier noted that similarities in jaw musculature suggested a relationship between shrikes and crows. From a study of the skull

and jaw muscles Bock (1963) concluded that the birds of paradise and bower birds are possibly related to the starlings and only convergently similar to the Corvidae.

Stallcup's (1961) serological comparisons indicated that *Lanius* is closer to the corvids than to any other of the species studied, but that the relationship is not a close one. He also found a strong serological reaction between *Parus* and the Corvidae. Stallcup's results, in this and in other problems, contain many inconsistencies and it is difficult to assess their true taxonomic value. Pocock (1966) found similar carpometacarpi in the Laniidae, Prionopidae, Dicruridae, Corvidae and some muscicapids. Robert Cook (personal communication) examined the carpometacarpi in six species of the Campephagidae and found that they agreed with the condition in the Corvidae, Laniidae and other groups in which Pocock's "process D" is absent. Bock (1962b) noted that the Corvidae, Oriolidae, Dicruridae, Grallinidae, Artamidae, Cracticidae, Ptilonorhynchidae and Paradiseidae have a single fossa in the head of the humerus. McFarlane (1963) found that the spermatozoa of the Corvidae and Laniidae are similar to one another and distinct from those of the non-oscines, swallows, vireos, fringillids and parulids.

The Type C egg-white patterns of the Corvidae are more similar to those of *Lanius* than to those of any other of the various groups which have been suggested as relatives. The corvids differ in virtually every respect from *Parus* and they are not sufficiently like the bulbuls, starlings, *Oriolus*, *Dicrurus*, the cracticids or the birds of paradise to support a claim of relationship. *Picathartes* also differs from the corvids. *Grallina*, although represented by a poor pattern, seems sufficiently different to be judged as not closely related.

The weight of evidence indicates that the Corvidae are convergently similar in certain characters to the Cracticidae, Paradiseidae and *Picathartes* but not closely related to them. Relationships to the other groups mentioned, except for *Lanius* and possibly the Campephagidae must be considered as unlikely. Thus *Lanius* emerges as a probable relative of the Corvidae and, if true, further evidence of this relationship will surely be found.

FAMILY CRACTICIDAE, Bell Magpies, etc. 2/11, fig. 10.

Species examined: *Gymnorhina tibicen*; *Strepera versicolor*.

The relationships of this group have long been a puzzle. Superficially they look like corvids or shrikes and in the earlier classifications, almost without exception, they were placed in or near the Corvidae or Laniidae. Pycraft (1907) however, concluded from a study of the skull, that *Gymnorhina* is related to the Artamidae and to the Paradiseidae. Leach (1914) made a detailed study of the myology, pterylosis and osteology of *Strepera* and concluded that it is related to *Gymnorhina* and *Cracticus*, not to the Corvidae. Clark (1945) noted that the pteryloses of *Cracticus* and *Strepera* are alike and also like those of the Paradiseidae. The pterylosis of *Grallina* he found to be somewhat like that of *Cracticus* but not importantly so.

Amadon (1951) monographed the Cracticidae and concluded that they are probably related to the Grallinidae, Ptilonorhynchidae, Paradiseidae and Cal-

laeidae but that a relationship to the Corvidae is uncertain. Amadon suggested that the Australian groups may be closer to such families as the Artamidae, Oriolidae and Dicruridae than to the Corvidae.

The egg-white patterns also indicate that *Gymnorhina* and *Strepera* are closely related. The sample of *Strepera* egg white was somewhat denatured and the conalbumins are difficult to see in the photograph but they are visible in the actual gel. The patterns of the two cracticids also show similarities to the pattern of the bird of paradise, *Diphyllodes*, especially in the ovalbumin region. The patterns of *Dicrurus* and *Oriolus* are somewhat similar to those of the Cracticidae but not any more so than to those of several other groups. The pattern of *Artamus* also shows certain similarities to *Gymnorhina*. The available pattern of *Grallina* (fig. 10) is not very good but it seems unlikely that fresh material would show a strong similarity to the cracticids.

It seems reasonable to conclude that the Cracticidae are probably related to the Paradiseidae, of uncertain affinities to several other groups, but not related closely to the Corvidae. If this is correct, and if Bock's (1963) suggestion that the Paradiseidae were derived from the Sturnidae is correct, we might expect to find some resemblance between the egg-white proteins of the Cracticidae and the Sturnidae. The patterns of the two groups are similar but several other families also have patterns grossly similar to those of the Cracticidae. The egg-white evidence therefore does not argue against Bock's suggestion but neither does it provide support.

FAMILY GRALLINIDAE, Magpie-larks. 1/4, fig. 10.

Species examined: *Grallina cyanoleuca*.

Shufeldt (1923) concluded from an osteological study that *Grallina* is unrelated to the Corvidae but that *Corcorax* is related to the corvid genus *Pyrhacorax*. *Struthidea* he thought to be related neither to the corvids nor to *Corcorax*. Amadon (1950a) placed both *Corcorax* and *Struthidea* in the Grallinidae and agreed with Shufeldt that *Grallina* is not related to the corvids but found the resemblances between *Corcorax* and *Pyrhacorax* to be due to convergence. Amadon believed the alliances of the Grallinidae to be with the Paradiseidae, Ptilonorynchidae, Callaeidae and perhaps the Cracticidae.

The egg-white pattern of *Grallina* was based on a denatured sample and the conalbumins are barely visible in the photograph. However, it seems unlikely that the complete pattern would closely resemble that of *Oriolus*, *Dicrurus*, the cracticids or the birds of paradise. With such poor evidence it is not profitable to speculate but the affinities of *Grallina* should remain an open question.

FAMILY PTILONORHYNCHIDAE, Bowerbirds. 0/17.

FAMILY PARADISEIDAE, Birds of Paradise. 2/43, fig. 10.

Species examined: *Paradisaea apoda*; *Diphyllodes magnificus*.

There is a considerable body of literature concerning the relationships of the bowerbirds to the birds of paradise and of these groups to other passerines. Stonor (1936, 1937, 1938) and Bock (1963) have reviewed the older accounts

and have added to the data on morphology, pterylosis, etc. Stonor (1937) concluded that these two families are not closely related to one another although Bock (1963) found evidence that they are closely related.

The literature and the egg-white protein data bearing upon the relationships of the Paradiseidae to other groups have been discussed above under the Corvidae and Cracticidae. I suggest that the Paradiseidae are probably related to the Cracticidae but are not close to the Corvidae. Bock's (1963) suggestion that the birds of paradise may be derived from the Sturnidae is neither confirmed nor denied by the egg-white evidence.

The egg-white pattern of *Diphyllodes* resembles, in some aspects, those of the Meliphagidae. An alliance between these two groups is zoogeographically probable and should be investigated.

FAMILY PARIDAE, Titmice. 13/64, fig. 10.

Species examined: *Parus atricapillus*, *major*, *ambiguus*, *niger*, *palustris*, *inornatus*, *caeruleus*, *lugubris*, *ater*; *Aegithalos caudatus*; *Psaltiriparus minimus*; *Auriparus flaviceps*; *Panurus biarmicus*.

FAMILY SITTIDAE, Nuthatches. 6/29, figs. 10, 11.

Species examined: *Sitta carolinensis*, *europaea*, *pusilla*; *Neositta chrysoptera*; *Climacteris picumnus*; *Tichodroma muraria*.

FAMILY CETHIIDAE, Creepers. 1/6, fig. 11.

Species examined: *Certhia familiaris*.

The relationships of the species listed above are conveniently discussed together. To what degrees the genera are related to one another is uncertain and the groupings into families have frequently been rearranged.

Gadow (1883) included *Parus*, *Aegithalos* (*Acredula*), *Psaltiriparus* (*Acredula*), *Auriparus* (*Aegithalos*), *Panurus*, *Regulus* and several other genera in his family Paridae. His doubts about the relationships of these genera were expressed in several places including a footnote (p. 3) which states that "*Panurus* does not belong to the Paridae, but perhaps to the Fringillidae."

Stresemann (1923) called attention to the presence of a complete post-juvenile molt in *Aegithalos*, *Psaltiriparus*, *Psaltria*, *Panurus* and *Paradoxornis*. *Aegithalos*, *Psaltiriparus* and *Psaltria* also share certain cranial characters, nest structure and naked hatchlings. *Parus* differs in all of these characters from the above genera. Delacour (1944) speculated that a line of relationships extends from the sunbirds (Nectariniidae) to the Dicaeidae which in turn are allied to *Remiz* and through *Remiz* to *Aegithalos*. Delacour believes that *Remiz*, *Aegithalos* and their allies are so different from *Parus* that they should not be in the same family with *Parus*.

Mayr and Amadon (1951) left the Paridae as a family but divided it into three subfamilies, Parinae, Remizinae and Aegithalinae but Mayr and Greenway (1956) did not recognize subfamilies in the Paridae. Vaurie (1957) objected to this arrangement and advocated the recognition of three separate families, Paridae, Remizidae and Aegithalidae. Vaurie also recorded the opinion of Delacour as follows (p. 2): "Mr. Jean Delacour, who for a long period has been giving

much thought to a classification of the passerine birds, tells me that in his opinion the penduline, long-tailed and true titmice represent three full families. He would place the Aegithalidae between the Paradoxornithinae on one side and the Paridae on the other in a sequence of families. He considers that the Paradoxornithinae are but a subfamily of the Muscicapidae, allied within this family to the Timaliinae, and would place in the Paridae only the true titmice. The Remizidae, which do not seem to be related at all to the Aegithalidae or Paridae, would then be placed next to the Dicaeidae."

Beecher (1953) placed the wren-tit (*Chamaea*), the parrot-bills (Paradoxornithinae) and the long-tailed tits (Aegithalinae) in the family Paradoxornithidae more or less adjacent to the families Troglodytidae, Certhiidae, Sittidae and Paridae. *Rhabdornis*, *Salpornis* and *Tichodroma* were included in the Certhiidae, *Climacteris* was believed to be a timaliid and *Tichodroma* was considered to possess characters indicating a link between the Certhiidae and Sittidae. *Remiz*, *Auriparus* and *Anthoscopus* were placed by Beecher in the family Paridae. Fiedler (1951) concluded from his study of jaw musculature that the Paridae are related to the Paradoxornithidae.

Mayr (1963) concluded from observations of the behavior of *Climacteris* that this genus is not related to *Certhia* and advocated its placement in a separate family, Climacteridae. Löhrl (1964) compared certain behavioral characters of *Parus*, *Aegithalos*, *Sitta*, *Tichodroma* and *Certhia*. He suggested that *Aegithalos* and *Psaltiriparus* should be separated from *Parus* in a separate family and that *Tichodroma* is related to *Sitta*, not to *Certhia*. Stallcup (1961) found that *Parus* is serologically most like *Cyanocitta* and *Turdus*. He did not compare the other genera under discussion. Greenway (1967) placed *Rhabdornis* and *Climacteris* in adjacent monotypic families and, in an understated footnote that clearly pertains to both, said (p. 161) "The relationships of this taxon are obscure." Greenway (p. 149) placed the monotypic subfamily Tichodromadinae in the Sittidae and the Salpornithinae in the Certhiidae. Snow (1967) recognized the families Aegithalidae, Remizidae and Paridae. These citations do not exhaust the supply of opinions about the relationships of these groups but they demonstrate the range of disagreements and also certain agreements. The egg-white data seem to support some of these opinions but to add further uncertainty in several cases.

The Type A electrophoretic patterns of the egg-white proteins of the species of *Parus* reveal a high degree of similarity and some specific variation. The patterns of *Parus major*, *P. ater* and *P. palustris* are virtually identical but *P. caeruleus* differs in the mobility of the conalbumin bands which move faster than those of the other species.

A search for patterns similar to those of *Parus* reveals that *Parus* and *Certhia* are much alike. The pattern of *Parus* is also much like that of the Fringillidae, especially the carduelines, and also like that of the Sylviidae. *Parus* and *Certhia* differ from the Troglodytidae in lacking a large, visible "ovomucoid," and in having weaker pre-albumins. However, they are similar in the albumin region. The presence or absence of an "ovomucoid" in this case is difficult to determine because *Parus* has a sharply defined band migrating just behind the ovalbumin region which could be an "ovomucoid." In the wrens this region contains a

larger, less well-defined fraction but whether or not these two components are homologous has not been determined. Comparisons between *Parus* and *Certhia* using paper electrophoresis also reveal similarities in pattern and in the mobilities of components.

When compared with *Aegithalos* and *Psaltriparus* it is apparent that *Parus* differs in several ways. The ovalbumin region in *Parus* is slower and there are differences within the ovalbumin region in the arrangement of the fractions. *Aegithalos* and *Psaltriparus* are identical to one another and their close relationship thus seems confirmed. Whether or not they should be separated from the Paridae and if so to what degree is a matter of taxonomic opinion. We may be looking at generic differences in many of these passerine problems and the boundaries of families may be outside the horizon of the group under discussion. For example, I can see resemblances between *Aegithalos* (including *Psaltriparus*) and *Sylvia* and, in gel #1830, *Certhia* and *Aegithalos* prove to have identical mobilities for component 18 and the conalbumins. The ovalbumins also show very similar mobilities but there are differences in the actual ovalbumin patterns. How are these facts to be assessed? Needless to say, with caution.

The pattern of *Panurus* differs from those of *Parus* and *Aegithalos*. It differs also from *Chamaea*, *Certhia*, *Tichodroma* and many other genera. *Panurus* is similar to *Climacteris* and also to several other genera including some of the thrushes. Resemblances between *Panurus* and the timaliids are not striking.

The pattern of *Sitta* differs markedly from those of *Parus*, *Certhia* and *Aegithalos*. *Tichodroma*, of which excellent patterns are available, also differs from *Sitta* in nearly every aspect of the pattern. A search for patterns similar to that of *Sitta* leads to some unlikely candidates including *Sturnus*, certain thrushes and sunbirds.

The electrophoretic pattern of *Climacteris* egg white is similar to that of *Sitta* in general outline but the details are difficult to assess. Since *Climacteris* and *Panurus* seem similar, it follows that *Sitta* is also similar to *Panurus*. In a general way this is true, but I do not find these resemblances entirely convincing because several of the patterns lack detail, probably due to denaturation. In summary, the similarities are certainly suggestive but they fall short, as usual, of providing proof. The differences indicate that *Sitta* is not really close to any of the genera mentioned.

Tichodroma usually has been placed either with *Sitta* or with *Certhia*. The egg-white pattern offers no clear support for either possibility. The pattern of *Tichodroma* egg white also differs from those of *Parus*, *Panurus* and *Climacteris*.

Certhia is another puzzle. In several aspects of its pattern it is similar to *Parus* and to the wrens, as noted above. However, the differences among these groups are also impressive and it is hazardous to speculate even though an alliance between *Certhia* and the wrens seems to be supported by other evidence. In the mobilities of component 18 and the conalbumins *Aegithalos* and *Certhia* match precisely but they differ in the ovalbumin region.

FAMILY CHAMAEIDAE, Wren-tits. 1/1, fig. 11.

Species examined: *Chamaea fasciata*.

In the original description of the wren-tit Gambel (1845) placed it in the genus *Parus* but two years later (1847) he erected the monotypic genus *Chamaea* in which the species has since remained. The wren-tit proved to be a troublesome object for family-level allocation and many of the early authors expressed their uncertainties. Baird (1858) was apparently the first to suggest that it might be allied to the babblers. He placed *Chamaea* in the subfamily Chamaeanae [*sic*] of the Liotrichidae (= Timaliidae). The wrens and mockingbirds were also included in this family. However, Baird (p. 370) noted that "I am not sure that I have correctly indicated the place of *Chamaea*, though there is no other family to which it could so readily be referred." Baird based his decision upon characters of the plumage (short, rounded wings; soft, lax plumage), the bill (short, compressed; long rectal bristles), and the legs and toes. By 1864 Baird had decided that *Chamaea* deserved family rank and he described the "Chamaeidae" (1864: 75). He noted that he had "found it impossible to assign . . . *Chamaea* to any recognized family of American birds . . . although it may properly belong to some old world group." Differences from the Paridae were noted as was its approach to "the Sylviidae in the sharp-ridged culmen and bristly gape, but it is otherwise very different." Baird concluded that "the family may, perhaps, be best placed between the Sylviidae and Paridae." Coues (1872) followed Baird in recognizing the Chamaeidae and placing it between the Sylviidae and Paridae.

Sharpe (1883) once again included the wren-tit with the babblers in his "Timeliidae" but this was a large assemblage that included birds which today are usually placed in the Turdidae, Sylviidae, Prunellidae, Ptilonorynchidae, Mimidae, Troglodytidae and Pycnonotidae. Sharpe (1883: 311) noted that "the wing is essentially Timeline, being concave and rounded, with a large first primary [= outer]; the legs too, are strong; but in other respects . . . the bird is Tit-like."

The first (1886) and second (1895) editions of the American Ornithologists' Union check-list of North American birds placed *Chamaea* in the subfamily Chamaeinae of the Paridae, along with *Psaltiriparus* and *Auriparus*. *Sitta* and *Parus* were in adjacent subfamilies. In subsequent editions the family Chamaeidae has been recognized.

The first examination of characters other than those visible in a museum skin was an osteological study by Lucas (1888) who concluded that both *Chamaea* and *Certhia* should be placed with the wrens. This was disputed by Shufeldt (1889a, b) who examined various anatomical characters, including pterylosis, and concluded that *Chamaea* is closest to *Psaltiriparus*. Shufeldt's evidence seems to have convinced Lucas who changed his mind (1891) and agreed with Shufeldt that *Chamaea* is more closely related to *Psaltiriparus* than to the wrens.

In 1896 Coues used the family Chamaeidae but noted that "the position and valuation of the group are still uncertain . . . and . . . it might be assigned to the Old World Timeliidae, with at least as much propriety as some other American groups, which have lately been relegated to that ill-assorted assemblage." These comments were presumably written before the appearance of the papers by Lucas and Shufeldt. Ridgway (1904: 684-5) reviewed the Lucas-Shufeldt debate concerning *Chamaea* and, although he recognized the Cha-

maeidae, noted that "it is possible that some so-called 'Timeliine' form of central or southern Asia may be found to be nearly related."

Coues (1903: 266) repeated the comments from his 1896 edition and noted that the arrangement presented in the 1886 and 1895 editions of the A.O.U. check-list (see above) had been arrived at "inadvertently" by the check-list committee. Wrote Coues "When doctors disagree like this, it is useless to exchange one dubiousity for another, and safest to continue the treatment the unfortunate patient has survived for some years." Coues therefore retained the family Chamaeidae but his further comments (1903: 281) made it clear that he had not abandoned the possibility that "the refractory genus *Chamaea*" might better be placed near the wrens and mockingbirds in a family including the babblers.

Reichenow (1914) placed *Chamaea* in the subfamily Parinae with *Parus*, *Aegithalos* (including *Psaltiriparus*), *Panurus* and several other genera. Reichenow's Paridae also included the genera *Paradoxornis* and *Polioptila* in other subfamilies.

For the next three decades the problem appears to have been ignored until Delacour (1946b) revised the Timaliidae and included *Chamaea* in the Tribe Chamaeini with *Panurus*, *Conostoma* and *Paradoxornis*. Like the earlier assignments of the wren-tit to the Timaliidae, Delacour's was based upon external characters of the plumage, bill and feet. Simmons (1957, 1961, 1963) has described several behavioral patterns which he has interpreted as indicating that the wren-tit is a babbler. Some recent authors, including Mayr and Amadon (1951), have accepted the allocation of *Chamaea* to the Timaliidae but others including Wetmore (1960) have retained the monotypic family Chamaeidae.

Although Beecher (1953: 315) noted that Delacour's proposal "is supported by internal characters" he preferred "to recognize the Paradoxornithidae as a family rather than to reduce the group to a tribe (Chamaeini) of the Timaliidae." Beecher also placed the subfamily Aegithalinae including *Psaltiriparus*, in the Paradoxornithidae. The characters cited by Beecher as supporting an alliance between *Chamaea* and the Paradoxornithidae are of uncertain value because *Chamaea* is noted as differing from *Paradoxornis* in several of the cited characters (bill, operculum, palate, tongue). Bock (1960: 450) found that *Chamaea* lacks the palatine process of the premaxilla while in typical timaliids it is present, although variable. In *Chrysomma* (= *Moupinia*) it is noted as "unfused, lying along the palatine." Bock (1962b) found that the double condition of the humeral fossa is only developing "in the Timaliinae (including *Chamaea*), the Sylviidae and the Muscicapidae." George (1962) found that *Chamaea* agreed most closely with the Sylviidae, *Sitta* and *Peucedramus* in the hyoid bones and muscles. However, he did not examine the condition in the babblers.

The proposal by Delacour (1946b) that *Chamaea* is a timaliid was based upon the external resemblance of the wren-tit to the Asiatic babbler, *Moupinia poecilotis*. If *Chamaea* is not a babbler, this superficial resemblance must be due to convergence and thus it is appropriate to search for species in other groups which resemble the wren-tit. One species that has impressed me in the field, and which shows similarities in museum specimens, is the Dartford warbler, *Sylvia undata*. Like *Chamaea* it inhabits dense thickets of the type called "chaparral" in California and "maquis" in the Mediterranean region. This plant forma-

tion is the product of the similar climates in the areas of principal abundance and the wren-tit and Dartford warbler are apparently convergently similar ecological counterparts. Both species reach the northern extremes of their ranges in more moist climates (Oregon, southern England), but even there they inhabit dense thickets. The behavior of the two species is generally similar, usually described as "skulking," with their long tails carried cocked up over the back. Both have bright irides (white in the wren-tit, reddish-orange in the Dartford warbler), build similar nests, and are highly vocal. In short, the superficial resemblances between *Chamaea* and *Sylvia undata* seem as impressive as those between *Chamaea* and *Moupinia poecilotis*. In both cases it seems likely that the similarities are due as much to convergence as to common ancestry.

Delacour (1946b: 11) expressed the opinion that the Sylviidae and Timaliidae are closely related, that a distinction between them is difficult, and that for some species it is not possible to decide to which of the two groups they belong. If this is true, the allocation of *Chamaea* becomes partly a matter of the definition of categorical boundaries. However, Delacour's opinion is apparently based upon external resemblances which may be due mainly to convergence.

If the above discussion accomplishes nothing more, it may help to provide a more neutral atmosphere in which to discuss the egg-white protein evidence. *Chamaea* has a relatively simple Type A egg-white pattern which lacks an obvious "ovomucoid" fraction. It also lacks any suggestion of a cathodal fraction. Component 18 is of average mobility, apparently somewhat slower than in most timaliids and the conalbumins are fairly close to component 18. The ovalbumin region is comparatively slow. In some patterns a faint pre-albumin area appears as in the sylviids, timaliids, and several other groups. The pattern of *Chamaea* differs from that of the typical timaliids (e.g., *Pomatorhinus*, *Pellorneum*, *Stachyris*, etc.) in lacking the cathodal element and in the slower mobilities of component 18, the conalbumins and the ovalbumins. The pattern of *Chamaea* resembles, more or less closely, those of *Sylvia*, *Prunella*, *Muscicapa*, *Motacilla* and others which lack an "ovomucoid" and a strong cathodal fraction. It differs markedly from that of *Panurus* which has a strong, well-separated "ovomucoid."

The egg-white evidence does not prove that *Chamaea* is not related to the Timaliidae, but it seems to me that the total evidence available fails to prove that it is. Neither does the egg-white evidence prove that *Chamaea* is a sylviid, but the total evidence suggests that it could be. The problem of the classification of *Chamaea* thus involves the usual difficulties, namely, the weighting of characters, the determination of genetic affinities, and the delineation of the boundaries of taxa. The various characters presently available seem to cancel one another out while modifications in the boundaries of categories do not solve problems of relationship. The important question of the genetic relationships of the wren-tit remains open and further evidence should be presented before the affinities of the wren-tit are considered to have been proved beyond doubt.

FAMILY TIMALIIDAE, Babblers. 10/260, fig. 11.

Species examined: *Pellorneum capistratum*; *Stachyris erythroptera*; *Pomatostomus superciliosus*; *Pomatorhinus montanus*; *Macronous gularis*; *Leiothrix lutea*; *Turdoides striatus*, *hypoleuca*, *plebeja*; *Picathartes gymnocephalus*.

The family Timaliidae has been especially difficult to define and its boundaries have been expanded or contracted by various authors for various reasons. Pycraft (1905c) proposed a large grouping of "turdiform" birds to include part of the Timaliidae plus the Pycnonotidae, Mimidae, Turdidae, Sylviidae, Parulidae, Regulidae, Cinclidae, Troglodytidae, Alaudidae and Motacillidae. Hartert (1910) placed the babblers, thrushes, Old World flycatchers and sylviiids as subfamilies in the Muscicapidae. Hartert's treatment was the basis for that of Delacour (1946b) who defined the subfamily Timaliinae on the basis of external form, habitat, general behavior, voice, juvenal plumage and food habits. He concluded that the babblers are closest to the Sylviinae and that it is extremely difficult to distinguish between the two groups. In Delacour's classification the Muscicapidae includes the subfamilies Timaliinae, Turdinae, Sylviinae, Muscicapinae, Pachycephalinae and Cinclosomatinae. The Timaliinae were divided into five tribes, Turdoidini, Chamaeini, Timaliini, Pomatorhini and Pellorneini. The wren-tit (*Chamaea*) and the bearded tit (*Panurus*) were placed in the tribe Chamaeini which Delacour proposed as the link between the babblers and the Aegithalinae-Parinae and then, in a sequential series, to the Remizidae, Dicaeidae and Nectariniidae. In a later paper Delacour (1950) commented on several genera and set up a sixth tribe, Picathartini, for *Picathartes* which he considered to be closest to the Turdoidini. Delacour and Amadon (1951) commented further on *Picathartes* and the evidence linking it to the Timaliidae, rather than to the Corvidae or Sturnidae.

Mayr and Amadon (1951) based their treatment on that of Delacour (and hence on Hartert) but enlarged their Muscicapidae to include the Muscicapinae (Old World flycatchers, monarchs, fantails, whistlers), Timaliinae (babblers, including *Chamaea*, *Panurus*, *Picathartes*, etc.), Sylviinae (warblers and gnatcatchers), Malurinae (Australian warblers), Turdinae (thrushes), Miminae (mockingbirds and thrashers), Troglodytinae (wrens) and Cinclinae (dippers). The Prunellidae and Motacillidae were included with the Muscicapidae in the "Primitive Insect Eaters."

Beecher (1953) interpreted his jaw muscle data as supporting Delacour's revision although he placed the babblers in the superfamily Timalioidea and the sylviiids in the superfamily Sylvioidea. This is a result of Beecher's designation of the Cisticolinae as the link between the two superfamilies. Beecher (1953: 321) believed the Timaliidae "to be a microcosm of the Timalioidea as well as the stem group from which its specialized families arose (the transitional Cisticolinae is as much a subfamily of Timaliidae as of Sylviidae). The best check on the evidence that the Timaliidae has given rise to shrike groups is seen in the existence of timaliine shrikes (*Pteruthius*, *Laniellus*). A good check on timaliid origin for other groups is seen in the occurrence of timaliine larks (*Cinclorhamphus*) in Australia where true larks do not occur. Similar examples are seen in what I interpret as timaliine titnices (*Parisoma*, *Myioparus*), creepers (*Clamateris*), and nuthatches (*Neositta*)." Although Beecher had at one time considered *Picathartes* to be similar to *Corvus* in its jaw musculature (Delacour and Amadon, 1951: 61), he later (1953: 313) agreed with Delacour and Amadon that *Picathartes* is timaliine.

Mayr and Greenway (1956) used an enlarged family Muscicapidae to in-

clude nine subfamilies as follows: Turdinae, Timaliinae (incl. *Chamaea*), Paradoxornithinae, Polioptilinae, Sylviinae, Malurinae, Muscicapinae, Monarchinae and Pachycephalinae. They gave family status to the Cinclidae, Troglodytidae and Mimidae, thus departing slightly from Mayr and Amadon (1951).

Delacour and Vaurie (1957) also included nine subfamilies in the Muscicapidae and differed from Mayr and Greenway (1956) only by including *Paradoxornis* in the Timaliinae and by recognizing a subfamily, Rhipidurinae, for the fantails. Amadon (1957) made adjacent families of the Timaliidae, Muscicapidae, Sylviidae, Turdidae, Mimidae and Troglodytidae. Wetmore (1960) retained the families of his earlier lists by recognizing the Paradoxornithidae, Chamaeidae, Timaliidae, Cinclidae, Troglodytidae, Mimidae, Turdidae, Zelandiidae, Sylviidae, Regulidae and Muscicapidae.

Simmons (1963: 191) examined several aspects of behavior in the babblers and concluded that the evidence from behavior "does not suggest a particularly close affinity with the thrush assemblage." Simmons cites some difficult genera which, although seemingly typical babblers, do not exhibit all of the behavioral attributes which he ascribes to the group. For *Chamaea*, however, Simmons entertains no doubt and concludes that "the behaviour evidence for the Wren-tit's being classed as a babbler is overwhelming."

Harrison and Parker (1965), also on the basis of behavioral characters, have proposed that *Malurus* and certain other genera be placed in the Timaliidae, rather than in the Muscicapidae. They also state their belief (1965: 105) that the Timaliidae, "appear to have close affinities, through *Paradoxornis*, with the long-tailed tits, Aegithalidae; and possibly through these to the penduline tits, Remizidae, and the true tits, Paridae, assuming that the assemblage of the three latter groups, now usually combined within the Paridae, is not polyphyletic."

The egg-white data agree with some of the above conclusions and disagree with others. First, it is of interest, and somewhat surprising, to find that the Type A patterns produced by the egg-white proteins of the typical babblers (*Pomatorhinus*, *Turdoides*, *Pellorneum*, *Stachyris* and *Macronous*) are virtually identical. This suggests at least that these genera, which Delacour (1946b) places in four different Tribes, are closely related to one another. Of particular interest is the presence of a cathodally migrating fraction, an unusual character in the passerines, although sometimes visible in concentrated samples in *Cisticola*, some fringillids, etc. It seems to be present in all the genera listed above although it is faint in some patterns and may not be visible in the published plates. Component 18 migrates more rapidly in the babblers than in most passerines, the conalbumins tend to move fast (except in *Stachyris*) and there is a well-marked pre-albumin.

Picathartes shares these characters with the typical babblers although its component 18 tends to be extremely faint. Thus the egg-white data support the conclusion of Delacour (1950) and Delacour and Amadon (1951) that *Picathartes* is a timaliid. The pattern of *Picathartes* egg white is less like that of the Corvidae and still less like that of the Sturnidae. Thus Sclater's (1930) opinion that *Picathartes* is a corvid and Lowe's (1938) that it is a sturnid are not supported.

The problem of the affinities of *Chamaea* has been discussed above. Because

of the consistency of the pattern among the typical babblers and the differences between them and *Chamaea* I believe it unlikely that *Chamaea* is closely related to the babblers, but this question must be examined with other techniques before any final conclusion can be drawn.

Panurus also differs from the typical babblers in its Type B egg-white pattern. It lacks the cathodal element, has a somewhat slower component 18 and, most impressively, has a well-marked "ovomucoid" region. It seems unlikely that *Panurus* and *Chamaea* are close enough to one another to be included in the same Tribe (Chamaeini) of the subfamily Timaliinae as advocated by Delacour (1946b) when they both differ considerably from the five genera of babblers listed above which are placed by Delacour in four different Tribes.

The relationships between the Sylviidae and the Timaliidae are uncertain. The egg-white patterns of the two groups have many features in common, including the cathodal component which can be seen in some concentrated sylviid patterns, e.g., *Cisticola*. The patterns of the two groups are Type A and they differ only in the mobilities of some fractions. Since the patterns of the Muscicapidae (and *Prunella*) are very similar to those of the Sylviidae, the same comments apply. *Pachycephala* and *Rhipidura* are discussed on page 74.

The relationships of the thrushes to the babblers raises the broader question of turdid-muscicapid-sylviid relationships which is better dealt with under those groups, but it does appear that the pattern exhibited by most thrushes differs from that of the babblers. There is no hint of a cathodal fraction in the thrushes, component 18 is slower than in the babblers, and the "ovomucoid"-ovalbumin region has a different arrangement.

Delacour (1946b) proposed that the babblers were allied to the long-tailed tits and *Parus* via *Chamaea*, *Panurus*, etc. Although I find no convincing evidence of a close relationship between *Chamaea* and *Panurus* or between either of them and the babblers, it is appropriate to examine the question of a babbler-titmouse relationship. *Aegithalos* and *Psaltiriparus* have a pre-albumin region that appears similar to that of the babblers but they differ in lacking the cathodal fraction and in the mobilities of component 18 and the conalbumins. The pattern of *Parus* differs in several respects from that of the babblers. The egg-white protein patterns of the Nectariniidae, which Delacour proposed as even more distant relatives of the babblers, are not like those of the babblers but resemble those of several other groups which, like the sunbirds, have a strong "ovomucoid" fraction.

A few conclusions and some suggestions can be proposed. The Timaliidae do seem to be a natural group probably composed of the species in Delacour's (1946b, 1950) tribes Pellorneini, Pomatorhini, Timaliini, Turdoidini, and Picathartini but not including *Chamaea* or *Panurus*. Whether or not the other genera of Delacour's tribe Chamaeini belong in the Timaliidae is another question. The closest relatives of *Chamaea* may prove to be the Sylviidae.

The babblers are probably not especially close to *Parus* but the similarities among the egg-white patterns of the babblers, sylviids and muscicapids may indicate relationship. The egg-white patterns of the thrushes are unlike those of the babblers in several respects but a relationship between them is not ruled out.

FAMILY CAMPEPHAGIDAE, Cuckoo-shrikes. 3/72, figs. 11, 12.

Species examined: *Coracina novaehollandiae*; *Lalage nigra*; *Campephaga phoenicea*.

The cuckoo-shrikes have long been recognized as an oscine family and in most of the older classifications (e.g., Sharpe, 1891; Shufeldt, 1904) and all of the recent ones (Berlioz, 1950; Mayr and Amadon, 1951; Mayr and Greenway, 1956; Delacour and Vaurie, 1957; Amadon, 1957; Storer, 1960; Wetmore, 1960) they are listed adjacent to the Pycnonotidae.

The cuckoo-shrikes are considered to be among the "more primitive" of the Old World insect eaters by Mayr and Amadon (1951). They suggest that the cuckoo-shrikes may be related to the bulbuls, possibly to the malaconotine shrikes and perhaps to the Dicruridae, Oriolidae and Irenidae. Since Amadon (1956) suggests that the Oriolidae may be related to the Sturnidae it follows that the possibility of a relationship between the cuckoo-shrikes and the starlings should also be considered. A relationship between the true shrikes (Laniidae) and the cuckoo-shrikes was often assumed in the older classifications but the resemblances between them have been ascribed to convergence by all recent authors.

Beecher (1953) concluded that the Campephagidae seem to have arisen from the Pycnonotidae and he allied the cuckoo-shrikes most closely with the waxwings, silky flycatchers and palm chats. Beecher also believed that the Calaeidae, Paradiseidae, Ptilonorychidae, Corvidae, Oriolidae, Nectariniidae, Dicaeidae and Zosteropidae were derived from the bulbuls and that the bulbuls are a subfamily of the Sylviidae.

Bock (1962b) found the condition of the pneumatic fossa of the humerus to be similar in the cuckoo-shrikes and bulbuls in which a second fossa is developing. The fossa is single in the Bombycillidae, Oriolidae, Dicruridae, Ptilonorychidae, Paradiseidae and Corvidae. It is double in the Dicaeidae, Nectariniidae and Zosteropidae.

As noted under the Corvidae, Robert Cook (personal communication) has found that "process D" (Pocock, 1966) is absent from the carpometacarpus in the Campephagidae, as it is in the Corvidae, Laniidae and several other groups.

The Type C egg-white pattern of *Campephaga phoenicea* is quite clear and it differs in several ways from the patterns of the species of *Pycnonotus*, *Dicrurus*, *Oriolus*, *Sturnus*, *Bombycilla*, *Phainopepla*, *Dulus*, and *Nectarinia*. The differences between *Campephaga* and *Pycnonotus* involve every portion of the patterns. Component 18 is relatively fast in *Campephaga* and the conalbumins are close to it. The opposite is true in *Pycnonotus*. In *Pycnonotus* there is an "ovomucoid" component which, in concentrated samples, merges with the ovalbumin to form a long, stained region. In *Campephaga* there is no obvious "ovomucoid" although there is a slower fraction behind the ovalbumin. The resulting patterns of the two groups are thus unlike in several respects. The samples of egg white from *Coracina* and *Lalage* were not in good condition. They produced poor patterns which seem to resemble that of *Campephaga*.

A search for patterns similar to that of *Campephaga* reveals nothing entirely convincing although some patterns of the Corvidae do show an ovalbumin

region similar to that of *Campephaga* and the slower part of the corvid pattern is also similar to that of *Campephaga*. The ovalbumin region in *Campephaga* is similar to that of *Sylvia* but these patterns also differ in details and the similarities could be coincidental.

Thus, while it would be unwise to assume a campephagid-corvid relationship or a campephagid-sylviid relationship because of these uncertain similarities, the differences between the bulbuls and *Campephaga* should be taken seriously. In themselves they do not prove lack of relationship but they at least reopen the question.

FAMILY PYCNONOTIDAE, Bulbuls. 16/109, fig. 12.

Species examined: *Pycnonotus atriceps*, *jocosus*, *leucogenys*, *aurigaster*, *xanthopygos*, *capensis*, *barbatus*, *finlaysoni*, *goiavier*, *blanfordi*, *brunneus*, *erythrophthalmos*, *importunus*, *milanjensis*; *Phyllastrephus terrestris*; *Hypsipetes philippinus*.

As Delacour (1943a) has noted, the bulbuls constitute one of the most clearly defined passerine groups. In Delacour's opinion the bulbuls are not close to the Old World flycatchers, thrushes, babblers, sylviids, or the other groups placed in the large family Muscicapidae by Delacour and Vaurie (1957) and some other authors. Delacour (1943a) briefly reviewed the older literature and commented upon the resemblances between certain bulbuls and birds of other families but he did not speculate upon their natural affinities. In the Delacour and Vaurie list (1957) the Pycnonotidae appear between the Campephagidae and the Irenidae and in the vicinity of the waxwings and their allies. As noted above under the Campephagidae (p. 64) virtually all authors have stated or implied a relationship between bulbuls and cuckoo-shrikes. The evidence for such an alliance is elusive and I have been unable to locate in diagnoses of the two groups any trustworthy characters which they share. On the contrary they seem to differ in most of the superficial characters usually cited. About the only similarity seems to be in the possession of abundant rump plumage but that of the cuckoo-shrikes has stiffened shafts and thus is convergently similar to that of the trogons and pigeons rather than to that of the bulbuls.

Harrison and Parker (1966) have proposed that the genera *Paramythia* and *Oreocharis* be transferred from the Dicacidae to the Pycnonotidae because of similarities in "general appearance, plumage pattern and colour, bill shape, tongue, stomach, and type of nest."

The egg-white pattern of the bulbuls is Type B with a well-defined "ovomucoid" fraction. In gel $\frac{+}{-}$ 2213 the bulbul pattern matches that of *Dicrurus* although there are differences in the mobilities of some components. The bulbul pattern is similar to that of *Oriolus* except that in *Oriolus* there is a strong pre-albumin which seems to be lacking in the bulbuls. The bulbul pattern also resembles that of *Sturnus*, the sunbirds and other groups with a Type B pattern. The bulbul pattern differs from those of *Campephaga* and the Timaliidae.

The relationships of the bulbuls may therefore be with the Dicruridae and possibly with the Sturnidae and Oriolidae but an alliance between the bulbuls and the Campephagidae is not supported by the egg-white evidence.

FAMILY CINCLIDAE, Dippers. 1/5, fig. 12.

Species examined: *Cinclus cinclus*.

The wrens and/or the thrushes have usually been assumed to be the closest relatives of the dippers although Shufeldt (1882) concluded from an osteological study that the parulid genus *Seiurus* is also close to *Cinclus*. The possession of a "booted" tarsus and a spurious tenth primary are the principal characters which are thought to ally the dippers with the thrushes. This alliance has long been accepted (e.g., Baird, 1864; Coues, 1884; Sharpe, 1891; Shufeldt, 1904) and was convincingly argued by Stejneger (1905). Ridgway (1904: 676) favored an alliance to both thrushes and wrens and viewed the wrens as possibly the closer relatives. In all of the more recent classifications the dippers have been placed near the thrushes and usually not far from the wrens. These two groups have been the allies most consistently proposed and there has been no important disagreement.

Mayr and Amadon (1951) placed the dippers as a subfamily in their large family Muscicapidae, which includes the thrushes, wrens, mockingbirds, etc. Ripley (1952) agreed that the dippers and thrushes are probably related and accepted the arrangement of Mayr and Amadon (1951).

The egg-white pattern of *Cinclus* in gel #2281 is similar to that of *Oenanthe* although the conalbumins of *Cinclus* are slower. The ovomucoid-ovalbumin region in *Cinclus* is similar to that of those thrushes which, like *Sialia*, have a tendency for the two fast fractions to merge in concentrated samples. Thus the egg-white evidence supports a dipper-thrush alliance but additional evidence should be sought before the question is considered settled.

The differences between the pattern of *Cinclus* and that of the wrens are so numerous that it seems unlikely that they are closely related.

FAMILY TROGLODYTIDAE, Wrens. 8/63, fig. 12.

Species examined: *Troglodytes troglodytes*, *aëdon*; *Thryothorus pleurostictus*; *Cistothorus palustris*; *Campylorhynchus brunneicapillus*, *jocosus*; *Uropsila leucogastra*; *Salpinctes obsoletus*.

A relationship between the wrens and the mimids has been accepted for a very long time. Lucas (1888) compared the skeletons of thrushes, mimids, and wrens and concluded that the Mimidae are intermediate between wrens and thrushes but he kept the three groups as separate families. Lucas also included *Certhia* and *Chamaea* in the Troglodytidae but later (1891) he agreed with Shufeldt (1889b) that *Chamaea* is not a wren.

Shufeldt (1889a) concluded from osteological evidence that the wrens are related to the mimids and thrushes. However, in this same paper, Shufeldt repeated the statement made in his 1882 paper that *Cinclus* is related to the water-thrushes (*Seiurus*: Parulidae). He also noted (1889a) that he found evidence showing that *Cinclus* is related to the wrens. Ridgway (1904: 475) stated that the relationships of the wrens "appear to be with the Mimidae on the one hand and Certhiidae on the other." In recent classifications (e.g., Mayr and Amadon, 1951; Wetmore, 1960) the wrens and mimids appear side by side. Although Beecher (1953) placed the wrens near the creepers in his superfamily

Timalioidea and the Miminae with the thrushes in the Sylvioidea he derived both groups from the Sylviidae. Stallcup (1961) concluded that his serological comparisons indicated that the wrens are not close to the mimids but that the wrens may be close to the genus *Parus*.

The egg-white patterns of the several species of wrens are impressively alike and indicate that the group is uniform in its egg-white characters. The egg-white protein patterns offer no support for a wren-mimid alliance. On the contrary, the differences between the two groups are so large and so consistently demonstrated by all available species, that it is reasonable to conclude that they are not as closely related to one another as each must be to some other group. The Type D patterns of the wrens show a strong, double pre-albumin, and an "ovomucoid" region, which make them quite unlike those of the Mimidae. Neither do the egg-white patterns support an alliance between the wrens and *Chamaea* or the wrens and the thrushes.

As discussed above under the Paridae, the Type A patterns of *Certhia* and *Parus* are similar to one another. The wren patterns show some similarities to those of the *Parus-Certhia* type although differences are also present. The resemblances do not constitute proof of a wren-*Parus-Certhia* relationship but neither do the differences deny the possibility.

The similarities between the pattern of *Geositta* and those of the wrens have been noted under the Furnariidae, p. 35. Whether or not these resemblances are significant can be resolved only by further studies which can eliminate or sustain the possibility that the similarities are coincidental.

FAMILY MIMIDAE, Thrashers, Mockingbirds. 8/30, figs. 12, 13.

Species examined: *Mimus gilvus*, *polyglottos*, *thenca*, *saturninus*; *Toxostoma rufum*, *curvirostre*; *Dumetella carolinensis*; *Melanotis caerulescens*.

The Mimidae have long been thought to be allied to the wrens on the one hand and to the thrushes on the other. The actual evidence for a wren-mimid relationship is more difficult to find. Lucas (1888) concluded from an osteological study of the three groups that the Mimidae fall between the wrens and thrushes but he also noted (p. 180) "that the Miminae should not be included in the very sharply-defined family Troglodytidae." As noted above, p. 67, the egg-white proteins of the Mimidae and Troglodytidae also differ in many respects and it seems reasonable to conclude that the two groups are not closely related.

The degree of relationship between the mimids and the thrushes is a more difficult question. Because all of the oscines are actually quite closely related to one another they share many characters or show but minor differences correlated with specialized adaptations. Thus, although it is possible to find both differences and similarities when comparing the anatomical characters of mimids and thrushes it is essentially impossible to evaluate their significance. Ripley (1952) reviewed the evidence and concluded that the differences between mimids and turdids are no more compelling than those between the turdids and the "other subfamilies of the Muscicapidae" i.e., muscicapids, sylviids and timaliids.

Beecher (1953) included the Miminae as a subfamily of the Turdidae which he derived from the Sylviidae. All other recent classifications have followed a similar pattern with the mimids either in or near the Turdidae. Stallcup (1961: 53) concluded that his serological evidence showed a relationship between mimids and *Turdus* although *Sturnus* and *Dendroica* showed a "greater serological correspondence to *Turdus* than does *Mimus*."

The Type A egg-white protein patterns of *Mimus*, *Toxostoma* and *Dumetella* are essentially identical except for minor variation in the mobilities of the conalbumins and component 18. The mimid pattern differs from that of most thrushes (e.g., *Turdus*, *Oenanthe*, *Erithacus*, etc.) because it lacks a visible "ovomucoid" fraction. Those patterns of the thrush genera *Sialia*, *Erythropygia*, *Cossypha* and *Copsychus* which are derived from concentrated samples appear more similar to the mimid pattern because the "ovomucoid" and ovalbumin regions tend to merge. Dilute specimens of *Sialia* however, reveal that a separate "ovomucoid" is present but dilute specimens of the mimids do not show a visible "ovomucoid." The mimid pattern is therefore Type A and an alliance with such groups as the Sylviidae should be considered as a possibility for further study.

FAMILY TURDIDAE, Thrushes. 46/304, figs. 13, 14, 15.

Species examined: *Turdus olivaceus*, *merula*, *pilaris*, *philemelos*, *libonyanus*, *viscivorus*, *rufiventris*, *grayi*, *albicollis*, *migratorius*, *poliocephalus*, *gurneyi*, *falklandii*, *plumbeus*, *fumigatus*, *torquatus*, *nudigenis*; *Erithacus rubecula*, *megarrhynchos*, *luscinia*; *Catharus occidentalis*, *aurantiiostris*, *fuscescens*; *Hylocichla mustelina*; *Oenanthe monticola*, *hispanica*, *lugens*, *leucura*, *leucomela*; *Cercomela familiaris*, *sinuata*; *Cossypha calfra*, *natalensis*, *heuglini*, *dichroa*; *Erythropygia barbata*, *coryphaeus*, *leucophrys*; *Phoenicurus phoenicurus*, *ochrurus*; *Myadestes townsendii*, *ralloides*; *Alethe diademata*; *Sialia sialis*; *Copsychus saularis*; *Chaimarrhornis leucocephalus*.

The history of the classification of the thrushes has been reviewed by Ripley (1952, 1962). At the family level many authors (Seeböhm, 1881; Seeböhm and Sharpe, 1898-1902; Pycraft, 1905c; Hartert, 1910; Mayr and Amadon, 1951; Ripley, 1952) have placed the thrushes either within the same family as the sylviine warblers and muscicapine flycatchers or adjacent to them. Most of these authors have also favored an arrangement that brings the babblers, mimids, wrens, dipper and *Prunella* into the vicinity of the thrushes, often as subfamilies within the same family. An arrangement that has gained considerable support is basically that of Hartert (1910) which includes in a large family Muscicapidae the subfamilies Turdinae, Sylviinae, Muscicapinae, Timaliinae, Miminae, Troglodytinae, Cinclinae and sometimes Prunellinae. About the only dissent raised against this approach was that of Witherby, Jourdain, Ticehurst and Tucker (1938) who objected more on the grounds that the enlarged group is unwieldy than that it is unnatural. Wetmore (1960) retained the above groups as separate families without comment.

The evidence for the alliance of these groups comes down to the fact that they are much alike in most anatomical characters, that some of the groups

seem to merge imperceptibly through intermediate species, and that the differences between them are few and inconstant. Thus, whether or not one agrees or disagrees with a particular arrangement depends upon the weight accorded to the similarities versus the differences.

A summary of some of the characters of the groups in question is presented below to indicate the nature of the evidence. The data have been drawn from various sources including Sharpe, 1879; Seebohm, 1881; Gadow, 1893; Hartert, 1910; Ridgway, 1904, 1907; Witherby et al., 1938; Ripley, 1952; Beecher, 1953; and Bock, 1962b.

All of these birds have ten primaries, the outer of variable development, and they also share numerous other characters of the suborder Passeres. The following outlines include some of the differences among these groups.

Turdidae: Juvenal plumage usually spotted; tarsus typically "booted" except lower portion and sometimes scutellate in young birds; single molt (in all species?); rictal bristles variable; jaw muscles similar to those of Mimidae and Cinclidae; humeral fossa double.

Sylviidae: Juvenal plumage unspotted; tarsus usually scutellate; double molt frequently present; rictal bristles variable; jaw muscles most similar to those of Muscicapidae and Pycnonotidae and not differing importantly from the Turdidae, Sturnidae and Hirundinidae; humeral fossa intermediate between single and double conditions.

Muscicapidae: Juvenal plumage usually spotted; tarsus scutellate; usually a single molt; strong rictal bristles; jaw muscles similar to those of Sylviidae and Turdidae; humeral fossa double.

Timaliidae: Juvenal plumage unspotted; tarsus scutellate; usually single molt; rictal bristles present; jaw muscles similar to those of Sylviidae, Motacillidae, Alaudidae and several other groups; humeral fossa intermediate.

Mimidae: Juvenal plumage unspotted; tarsus scutellate; single molt; rictal bristles present; jaw muscles as in the Turdidae; humeral fossa double.

Cinclidae: Juvenal plumage unspotted; tarsus "booted"; single molt; rictal bristles absent; jaw muscles similar to those of Turdidae and several other groups; humeral fossa double.

Troglodytidae: Juvenal plumage unspotted; tarsus scutellate; single molt; rictal bristles absent or not well-developed; jaw muscles similar to those of *Certhia*, *Parus*, *Sitta* and *Malurus*; humeral fossa intermediate with second fossa forming.

Prunellidae: Juvenal plumage unspotted; tarsus scutellate in front some scales more or less fused; single molt; rictal bristles absent; jaw muscles similar to those of Turdidae; humeral fossa double.

To a person uncommitted to any particular viewpoint the characters listed above will not seem compelling either as indications of relationship or the lack of it. The value of tarsal scutellation as a taxonomic character has been brought into question by several authors (Pycraft, 1906; Błaszyk, 1935; Plotnick and Pergolani de Costa, 1955; Rand, 1959) and the development of rictal bristles is clearly correlated with food habits. The jaw muscle data of Beecher (1953) do

not seem trustworthy as a basis for determining natural groups at this level for there are too many resemblances between groups otherwise seemingly unrelated. Bock (1962b) has concluded that the taxonomic value of the humeral fossa cannot, as yet, be assessed. The spotting of the juvenal plumage in most thrushes and many flycatchers becomes a significant character only because such spotting is rare outside these groups. Whether or not the sharing of this condition is indicative of relationship or convergence is, at present, simply not known.

The significance of one versus two molts per year is certainly adaptive and there are exceptions to the "rule" in both the Sylviidae and the Turdidae. It thus seems clear that those who advocate the inclusion of these several groups within a single family do so because they share many attributes and differ only in characters which are inconstant. Since it is generally agreed that the passerines are usually divided into more families than is justified in comparison with the non-passerines it is logical to merge passerine families when the evidence permits. I have commented upon this problem in the Introduction and have expressed support for this viewpoint.

The egg-white protein data raise some additional questions but they also reveal some clusters of possibly related groups. Following are descriptions of the electrophoretic patterns of the egg-white proteins of the groups in question.

Turdidae: Most of the thrushes, including *Turdus*, *Catharus*, *Hylocichla*, *Myadestes*, *Oenanthe*, *Erithacus*, *Luscinia*, *Phoenicurus* and *Cercomela* have Type B patterns with two distinct sets of proteins migrating anodally beyond the conalbumins. The faster of these is probably the ovalbumin; the slower, in a non-passerine pattern, would be assumed to be the ovomucoid fraction but there is no evidence that this is actually ovomucoid in passerines. The ovalbumin region is composed of several fractions as indicated by some of the more dilute specimens of *Phoenicurus* and *Oenanthe*. The "ovomucoid" region seems to be a single diffuse fraction. In *Sialia*, *Erythropygia*, *Copsychus* and *Cossypha* there is no readily observable separation between the ovalbumin region and an "ovomucoid" fraction in concentrated samples. Thus these four genera sometimes show a large but single fast region. In gel #2264 a dilute specimen of *Sialia* shows a clear separation between the ovalbumin and an "ovomucoid" region, as in other thrushes. Thus the apparent difference is due to a relatively minor change in mobility which results in the merging of the two fast fractions except in very dilute specimens.

Sylviidae: The pattern of the typical sylviids is Type A as found in *Sylvia*, *Phylloscopus*, *Hippolais*, *Cisticola*, *Malurus*, and *Orthotomus*. This pattern differs from the *Turdus* type pattern in having a single set of fractions migrating ahead of the conalbumins in the ovalbumin region. In other words, these sylviids lack the "ovomucoid" fraction of *Turdus* and most other thrushes. The pattern of *Sylvia* etc. matches, in detail, that of *Muscicapra* and it is also a good match for those of *Prunella*, *Motacilla*, *Anthus*, *Chamaea*, *Mimus*, *Certhia*, *Aegithalos*, *Psaltiriparus*, *Zosterops*, *Vireo* and the "nine-primaried oscines" (= Fringillidae of this paper).

The genus *Prinia* presents a special problem. Egg white is available from five species, three of which (*maculosa*, *robertsi* and *subflava*) show a typical sylviid pattern. *P. socialis* and *P. flaviventris* however, have two fast fractions, thus resembling the turdid pattern. It is clear from an examination of patterns produced by samples of different concentrations that the "ovomucoid" band in the *Prinia* patterns has the same mobility as the "ovalbumin" band in the sylviids and that the fastest ("ovalbumin") fraction in *Prinia* has the same mobility as the "pre-albumin" of the sylviids. Thus the "ovalbumin" of the sylviids may actually be homologous to the "ovomucoid" of the turdids and the "pre-albumin" of sylviids may be the homolog of the "ovalbumin" of the turdids. These homologies are suggested by the patterns of *Prinia socialis* and *P. maculosa* in gel #2272. In the *socialis* pattern the faster of the two fractions is the stronger while in the *maculosa* pattern the slower is the most dense. Thus the *socialis* pattern is like that of the turdids and that of *maculosa* is like a sylviid pattern with strong "pre-albumins."

The situation in *Prinia* suggests that the real difference between the sylviid and turdid patterns may be due to the relative amounts of the two fast components, i.e., in the turdids there is a high concentration of the fastest fraction but in the sylviids it usually occurs in a low concentration. The observed differences between the two groups are sufficiently consistent to consider them to be significant but the actual genetic difference between Type A and Type B patterns may be small. Another possibility is that *Prinia* is not especially close to the Sylviidae. McLachlan and Liversidge (1957) place it in a separate family, Priniidae, because it has only ten rectrices and nests and eggs unlike those of the Sylviidae.

Some patterns of *Acrocephalus* also show two components in the "ovomucoid"—ovalbumin region. However, the mobilities in *Acrocephalus* seem to be like those of the typical sylviids; in *Prinia* the faster fraction approaches the mobility of the ovalbumin in the turdids.

The pattern of the Australian genus *Acanthiza* differs markedly from that of the typical sylviids. *Acanthiza* is discussed below under the family Sylviidae.

Muscicapidae: The Type A pattern of *Muscicapa*, as noted above, matches that of *Sylvia* in detail and also that of *Prunella*, *Motacilla*, etc. *Muscicapa* is compared with *Rhipidura* and *Pachycephala* on page 74.

Prunellidae: The Type A pattern of *Prunella* is not distinguishable from those of *Sylvia* or *Muscicapa* but it is readily separated from the Type B patterns of *Turdus* and other thrushes. Although Beecher (1953) placed *Prunella* in the Turdidae, and Ripley (1952) agreed, the jaw musculature of *Prunella* does differ somewhat from that of the typical thrushes (Beecher, 1953: 281). *Prunella* has scutellate tarsi and the fact that the immature plumage is streaked or mottled hardly seems like a solid basis for a family-level allocation. If nothing more the egg-white evidence re-opens the question of the relationships of *Prunella*.

The egg-white patterns of the Timaliidae, Mimidae, Cinclidae and Troglodytidae have been discussed earlier.

From a consideration of all of the available evidence it seems reasonable to conclude that:

- 1) The thrushes form a natural group which share many anatomical characters with other groups of passerines but which do not seem to be as closely related to the Sylviidae, Muscicapidae and Prunellidae as these three groups, and perhaps others, are to one another.
- 2) The thrushes do not seem to be especially close to the babblers but, as noted above under the Timaliidae the two groups may be related to one another more closely than either is to most other passerine groups. However, each can also be defined by egg white and other characters not shared between them and the degree of relationship involved is simply not yet known.
- 3) The thrushes seem relatively distant from the Troglodytidae.
- 4) The thrushes are probably related to the Cinclidae but a close relationship between the thrushes and the Mimidae seems less certain and further evidence is needed.

FAMILY ZELEDONIIDAE, Wrenthrushes. 1/1, fig. 28.

Species examined: *Zeledonia coronata*.

See Tribe Zeledoniini, Subfamily Emberizinae, Family Fringillidae. p. 106.

FAMILY SYLVIIDAE, Old World Warblers. 48/395, figs. 15, 16, 17.

Species examined: *Sylvia borin*, *communis*, *curruca*, *melanocephala*, *nana*, *nisoria*, *currucoides*, *atricapilla*; *Prinia socialis*, *flaviventris*, *robertsi*, *maculosa*, *subflava*; *Acrocephalus scirpaceus*, *gracilirostris*, *baeticatus*, *schoenobaenus*; *Phylloscopus trochilus*, *collybita*, *sibilatrix*; *Cisticola fulvicapilla*, *galactotes*, *chiniana*, *juncidis*, *ayersii*, *textrix*, *tinniens*, *natalensis*, *aberrans*; *Acanthiza pusilla*, *hedleyi*, *hamiltoni*, *uropygialis*, *chrysorrhoea*; *Sylvietta rufescens*, *brachyura*; *Orthotomus sutorius*, *sericeus*; *Malurus cyaneus*; *Lusciniola melanopogon*; *Locustella naevia*; *Hippolais polyglotta*, *icterina*; *Camaroptera brachyura*; *Apalis thoracica*; *Bradypterus babaeculus*; *Euryptila subcinnamomea*; *Epthianura tricolor*.

FAMILY REGULIDAE, Kinglets. 1/4.

Species examined: *Regulus regulus*.

The Sylviidae have been discussed and compared above under the Paridae, Chamaeidae, Timaliidae, Cinclidae, Troglodytidae, Mimidae and, especially, under the Turdidae. To these discussions little more need be added but the evidence may be summarized as follows:

- 1) The egg-white pattern of *Sylvia* and other "typical" sylviids is quite simple and thus the probability of coincidental similarities is increased. This problem should be kept in mind when assessing resemblances to the patterns of other groups.
- 2) The patterns of *Muscicapa* and *Prunella* are excellent matches for that of *Sylvia*.
- 3) The patterns of *Motacilla*, *Anthus*, the swallows, the larks, *Parus*,

Certhia, *Psaltiriparus*, *Aegithalos*, *Chamaea*, the mimids, *Passer*, *Vidua*, *Zosterops*, *Vireo*, the "nine-primaried oscines" and other type A groups resemble that of *Sylvia* to various degrees.

- 4) The patterns of *Turdus*, *Catharus*, *Erithacus* (etc.), *Sitta*, *Pycnonotus*, the wrens, starlings, and other groups having Type B patterns differ from that of *Sylvia*.
- 5) The variation in pattern types within the genus *Prinia* raises a question concerning the significance of the otherwise impressively consistent differences between Type A and Type B patterns. This problem may be solved, in part, by a determination of the homologies of the fractions in the different types of patterns.
- 6) The pattern of *Acanthiza* differs from that of *Sylvia* and resembles those of certain honeyeaters.

It seems reasonable to conclude that the Sylviidae (except perhaps *Acanthiza* and *Prinia*) are closely related to the Muscicapidae (in the restricted sense) and to *Prunella*. Other relatives, possibly close, may include *Chamaea*, *Aegithalos*, *Psaltiriparus* and the Motacillidae. The degrees of relationship to other groups with similar egg-white patterns are unknown. The Sylviidae, Muscicapidae and Prunellidae are probably more closely related to one another than any one of them is to the Turdidae.

The suggestion by Harrison and Parker (1965) that *Malurus* is a timaliid because of certain behavioral similarities is not supported by the protein evidence. The pattern of *Malurus cyaneus* is an excellent match for that of *Sylvia* and differs from those of the babblers.

The patterns of *Acanthiza hamiltoni* and *A. chrysorrhoa* differ so much from those of *Sylvia* and other typical sylviids that it seems unlikely that *Acanthiza* is a sylviid genus. The pattern of *Acanthiza* is similar to those of *Lichmera* (Meliphagidae) and *Pardalotus* (Dicaeidae). These resemblances introduce the possibility that these Australian genera are related to one another and that *Acanthiza* is only convergently similar to the Sylviidae. Further evidence for and against this hypothesis should be sought.

The pattern of *Epthianura tricolor* is similar to that of the sylviids but even more like the *Meliphaga* type of pattern in which the conalbumins are slightly faster and the pre-albumin is more pronounced. This poses a question similar to that presented by *Acanthiza*, namely, is it possible that *Epthianura* is more closely related to *Meliphaga* than to *Sylvia*?

The available patterns of *Regulus* are not of good quality but they appear to match those of *Sylvia* and other typical sylviids. Whether or not a family Regulidae is recognized is a matter of taxonomic opinion.

FAMILY MUSCICAPIDAE, Old World Flycatchers. 26/378, figs. 17, 18.

Species examined: *Muscicapa striata*, *narcissina*, *tricolor*, *adusta*; *Ficedula hypoleuca*; *Oreoica gutturalis*; *Terpsiphone viridis*, *paradisi*; *Parisoma plumbeum*, *subcaeruleum*; *Bradornis pallidus*; *Dioptornis fischeri*; *Seisura inquieta*; *Platysteira peltata*; *Rhipidura fuliginosa*, *perlata*, *leucophrys*, *javanica*; *Pachycephala pectoralis*; *Colluricincla harmonica*, *rufiventris*; *Batis capensis*;

Melaenornis pammaelina; *Chloropeta natalensis*; *Trochocercus cyanomelas*; *Sphenostoma cristatum*.

The relationships of the Muscicapidae have been discussed above under the Turdidae and Sylviidae. The evidence from various sources, including the egg-white protein patterns, suggests that the typical muscicapids (e.g., *Muscicapa*) are closest to the Sylviidae and perhaps to *Prunella*. Since the Muscicapidae are thought to be close to the Sylviidae it follows that they are also related to those other groups (Motacillidae, *Chamaea*, etc.) which seem to show affinities with the sylviids. Also the muscicapids seem less closely related to the thrushes than to the Sylviidae and *Prunella*.

Pocock (1966), on the basis of the presence or absence of a certain process ("Process D") on the carpometacarpus has suggested that the Muscicapidae may be polyphyletic. The genera *Batis* and *Terpsiphone* lack the process and thus agree with the Laniidae, Prionopidae, Dicruridae and Corvidae. Several other genera of South African flycatchers possess the process in common with most other passerine groups.

The degree of relationship between the typical flycatchers (*Muscicapa*, *Ficedula*, etc.) and the fantails (*Rhipidura*) and whistlers (*Pachycephala*) is uncertain. Some recent authors have separated them as tribes, subfamilies or even families. The Type B pattern of *Rhipidura* has a clear "ovomuroid" fraction and thus differs markedly from the patterns of the typical muscicapids. In side by side comparisons the pattern of *Rhipidura* is similar to that of other Type B groups including *Pycnonotus* although they differ in the mobilities of some fractions. The pattern of *Rhipidura* differs even more from that of *Turdus*. The *Rhipidura* pattern is an excellent match for that of *Sphenostoma* (see below) and is possibly similar to that of *Pachycephala* but the available patterns of the latter are not good enough for critical comparison.

The Australian genus *Sphenostoma* has been placed in various families including the Paridae, Falcunculidae (Serventy and Whittell, 1967) and in a family Sphenostomidae (with *Aphelocephala*) by Mathews (1923-24). Deignan (1964) included *Sphenostoma* in the Orthonychinae of the Muscicapidae. The egg-white pattern of *Sphenostoma cristatum* (see gel # S-2450) is quite unlike that of *Parus*. In addition *Sphenostoma* has a loud, ringing song performed by both sexes and lays blue eggs in an open nest (Mathews, 1923-24). It thus seems clear that the superficial resemblances between *Parus* and *Sphenostoma* are due entirely to convergence.

The egg-white pattern of *Sphenostoma* is also unlike that of the typical muscicapids but it does resemble that of *Rhipidura*. This resemblance extends to having the same or extremely similar mobilities for all components. They seem to differ only in the relative amounts of the "ovomuroid" fraction which occurs at a lower relative concentration in *Sphenostoma*. A close relationship between *Rhipidura* and *Sphenostoma* is thus a possibility and further evidence should be sought.

FAMILY PRUNELLIDAE, Accentors. 1/12, fig. 18.

Species examined: *Prunella modularis*.

The genus *Prunella* seems to combine the characters of buntings, flycatchers and thrushes. In appearance the accentors resemble emberizine finches but the tenth primary is present and the bill is somewhat thrushlike. The nostrils are operculate, the tarsus is short and scutellate in front. A true crop and a muscular gizzard are present. The eggs are dark blue-green which is taken as one of the thrushlike characters. Like buntings, *Prunella* feeds in part on seeds.

The relationships of *Prunella* have been discussed above under the Turdidae and Sylviidae. I suggest that *Prunella* is possibly closer to the Sylviidae and Muscicapidae than to the thrushes. A relationship to the Motacillidae and to the other groups mentioned under the Sylviidae is also possible.

Udagawa (1954) compared the chromosome patterns of *Prunella* and *Luscinia calliope*. He concluded that they are sufficiently similar to warrant placing *Prunella* in the Turdidae. However, they also differ and Udagawa fails to present a convincing case because he does not offer comparisons with enough other groups to establish the significance of the similarities and differences between *Prunella* and *Luscinia*.

FAMILY MOTACILLIDAE, Wagtails, Pipits. 14/48, figs. 18, 19.

Species examined: *Motacilla flava*, *cinerea*, *alba*, *capensis*, *grandis*; *Macronyx croceus*; *Anthus novaezeelandiae*, *leucophrys*, *trivialis*, *bertholti*, *pratensis*, *spinolletta*, *correndera*, *antarcticus*.

The Motacillidae may be diagnosed as small terrestrial Passeres with nine primaries, resembling larks in appearance but with an acutiplantar tarsus the sides of which are covered by an unbroken sheath; the acrotarsium is more or less distinctly scutellate. The tertials are conspicuously elongate; bill slender and notched; hind claw long and straight; rectal bristles present; nostrils operculate.

Here again is a set of characters shared in various combinations with other groups. Convergence with the larks and other ground-dwellers is indicated by some features but the true relationships of the group are obscure. Mayr and Amadon (1951: 21) suggested that the motacillids probably "are modified descendants of some group of turdids or sylviids, and they are best placed following this group of families."

Beecher (1953) interpreted his comparisons of jaw musculature as indicative of a natural relationship between pipits and larks with both derived from the sylviids. The Timaliidae and Paradoxornithidae are also considered by Beecher to be related to the pipits and larks.

The egg-white patterns of *Motacilla* and *Anthus* agree in all species. The apparent differences visible in the plates are due to a combination of real mobility differences and the effects of different sample concentrations. The pre-albumin area visible in concentrated samples is actually present in all species.

The motacillid pattern is Type A like that of the other groups which lack an "ovomucoid" fraction, including the sylviid—muscicapid complex. Thus they differ from the turdids which have an "ovomucoid" component.

The affinities of the motacillids seem most probably to be with the Sylviidae and Muscicapidae. The pointed, nine-primaried wing is apparently correlated with the long migratory flights of the species of this group (Averill, 1925;

Stegmann, 1962) and does not necessarily indicate relationship to other nine-primaried passerines. However, the egg-white pattern of the motacillids is quite similar to that of the emberizines, carduelines, etc. and an alliance between these groups should not be ruled out without seeking further evidence.

The egg-white patterns of the Alaudidae and Motacillidae are generally similar and a relationship between these two groups is possible. However, they also differ in the relative mobilities of the conalbumins and component 18. These are small and rather subtle differences of uncertain significance but the overall effect is to produce a greater similarity between the sylviids and motacillids than between the latter and the larks. Clearly this is another case where more convincing evidence is required.

Support for a relationship between the motacillids and the Paradoxornithidae (*Panurus*) is lacking in the egg-white data.

FAMILY BOMBYCILLIDAE, Waxwings. 1/3, fig. 19.

Species examined: *Bombycilla cedrorum*.

FAMILY PTILOGONATIDAE, Silky Flycatchers. 1/4, fig. 19.

Species examined: *Phainopepla nitens*.

FAMILY DULIDAE, Palm Chat. 1/1, fig. 19.

Species examined: *Dulus dominicus*.

These three groups are considered together because they are often thought to be related. Arvey (1951) concluded from a study of the skeleton, certain muscles and the digestive tract that the waxwings, silky flycatchers and the palm chat were closely related and should be included in a single family. As Arvey (1951: 477) noted, this is not a novel idea for most workers prior to 1900 had included these groups in the family Ampelidae. Ridgway (1904: 113) proposed their separation as three families. Delacour and Amadon (1949) also treated the three groups as a single family and included *Hypocolius* as a fourth subfamily in the Bombycillidae. Mayr and Amadon (1951) followed this arrangement but Amadon (1956) later expressed uncertainty about the relationship of *Hypocolius* to the waxwings. Beecher (1953) interpreted his jaw muscle data as indicating that the waxwings, silky flycatchers, palm chat and *Hypocolius* are related to one another and to the Campephagidae and Pycnonotidae. Bock (1962b) noted that the humeral fossa is single in the "Bombycillidae (including *Dulus*)" and also in the Artamidae. Wetmore (1960) retained the Bombycillidae, Ptilogonatidae and Dulidae as separate but adjacent families. He cited skeletal differences and the communal nesting habits of *Dulus* as the basis for this arrangement. Thus, there is general agreement that these groups are related to one another but some disagreement as to the degree of relationship and its categorical expression.

The Type B egg-white patterns of *Bombycilla* and *Phainopepla* are similar although the available pattern of *Phainopepla* is not very good. The pattern of *Dulus*, although Type B by definition, differs markedly from those of *Bombycilla* and *Phainopepla* and the differences are sufficient to cast doubt on a close relationship between *Dulus* and the other two genera.

A search for other patterns similar to those of *Bombycilla* and *Phainopepla* reveals a number that show some features in common but none that is convincing. The patterns of *Bombycilla*, *Phainopepla* and *Dulus* all differ from that of *Campephaga*. *Dulus* shows some similarity to *Pycnonotus* but it is not sufficient to be considered significant. A search for patterns similar to that of *Dulus* fails to discover any convincing resemblances.

The egg-white evidence thus appears to support a relationship between *Bombycilla* and *Phainopepla* but not between these and *Dulus*.

FAMILY ARTAMIDAE, Woodswallows. 2/10, fig. 19.

Species examined: *Artamus personatus*, *fuscus*.

The species of *Artamus* occur from Australia and New Guinea to Indonesia, India and the Philippines. They are morphologically uniform and differ from other passerines in the structure of the bill and the presence of powder-downs. The woodswallows are primarily insectivorous, capturing flying insects somewhat in the manner of swallows. They also forage from a perch as do flycatchers and sometimes feed on the ground where they may take seeds as well as insects. They nest in a variety of places including open sites, the abandoned nests of other birds and cavities. The nests are constructed of twigs, grasses, fibers and feathers, and the eggs are whitish or greenish and variously spotted and streaked. In short, although the woodswallows are well differentiated there are no obvious clues to their relationships and, as noted by Immelmann (1966: 37), the systematic position of the group is not yet clear. Many groups have been suggested as possible relatives of *Artamus* including the Hirundinidae, Laniidae, Oriolidae, Sturnidae, Bombycillidae, Vangidae, Cracticidae and Paradiseidae.

Sharpe (1890: 1) placed the Artamidae next to the Sturnidae and noted that "the Artamidae may be a Sturnine family, but of that I am not yet assured." Pycraft (1907) considered *Artamus* to be related to *Gymnorhina* and the Paradiseidae based upon a study of the skull. Amadon (1951) thought that *Artamus* may be close to the Cracticidae and Mayr and Amadon (1951) noted that "the relationships of *Artamus* are doubtful, but there is a certain resemblance to some of the Vangidae and even to the Bombycillidae." Beecher (1953) placed the Artaminae in the Cracticidae in which he also included *Pityriasis* and *Grallina*. Beecher (1953: 296) noted that "internal characters and the black-and-white plumage patterns unite the groups." Bock (1962b) found a single humeral fossa in *Artamus* which agrees with the condition in the Oriolidae, Grallinidae, Cracticidae, Paradiseidae, Laniidae, Bombycillidae and some Sturnidae. A second fossa is developing in the Hirundinidae.

The Type B egg-white protein pattern of *Artamus* matches that of *Sturnus* in remarkable detail. (See gel # S-2386). They differ only slightly in the mobilities of component 18 and the conalbumins. The pattern of *Artamus* is less like those of *Bombycilla*, *Gymnorhina*, *Cracticus*, *Oriolus* and *Diphyllodes*. It is still less like those of the swallows and shrikes.

The close resemblance between the egg-white patterns of *Artamus* and *Sturnus* does not prove close relationship but it does provide a stimulus to search for additional evidence. Thus, after 78 years, I can only agree with Sharpe's

statement that the Artamidae may be related to the starlings, "but of that I am not yet assured."

FAMILY LANIIDAE, Shrikes. 15/67, figs. 19, 20.

Species examined: *Lanius collurio*, *ludovicianus*, *excubitor*, *excubitorides*, *colaris*, *senator*; *Laniarius atrococcineus*, *ferrugineus*; *Telophorus quadricolor*, *zeylonus*; *Tchagra australis*, *senegala*; *Nilaus afer*; *Chlorophoneus sulphureopectus*; *Urolestes melanoleucus*.

The relationships of the shrikes involve the usual twin problems of which genera should be included in the Laniidae and to which other families they are related. Both questions are complicated by the frequency of convergence in the evolution of the shrike-like bill. Mayr and Amadon (1951) discussed this problem and noted that at one time or another various genera assigned to the Laniidae have been placed in the Pachycephalinae, Campephagidae, Vireonidae, Cracticidae, Vangidae, and Prionopidae. Mayr and Amadon (1951) expressed doubt concerning the relationship between the African bush shrikes (*Malaconotus*, *Chlorophoneus*, *Telophorus*, *Tchagra*, *Laniarius*, etc.) and the genera *Lanius*, *Urolestes* and *Corvinella*. Mayr (1943) assigned *Nilaus* to the Muscicapidae. Beecher (1953) interpreted his jaw muscle data as indicating a relationship between *Lanius* and *Malaconotus* and derived his Laniidae from the Monarchidae. However, Fiedler (1951) interpreted his jaw muscle data as indicative of a laniid-corvid relationship and Jollie (1958) noted that Beecher's drawings of the jaw muscles of the Corvidae are like those of *Lanius* and *Oriolus*. Bock (1962b) noted that *Lanius* has a single humeral fossa, a condition shared with the Corvidae, Bombycillidae, Dulidae, Oriolidae, Dicruridae, Grallinidae, Artamidae, Cracticidae, Ptilonorhynchidae and Paradiseidae. The spermatozoa of the Corvidae and Laniidae are also similar (McFarlane, 1963). Pocock (1966) found that the Laniidae, Prionopidae, Dicruridae, Corvidae and the muscicapid genera *Batis* and *Terpsiphone* agree in lacking "Process D" on the carpometacarpus. This process is present in many other passerine groups.

Type C egg-white patterns of *Lanius* seem more like those of the Corvidae than of any other available group. However, the patterns of both groups tend to be unusually simple and thus the probability of coincidental similarity is high. Although the weight of evidence suggests that a corvid-laniid relationship is possible it has not been proved beyond doubt and further evidence must be obtained before this alliance is accepted.

The patterns of *Telophorus quadricolor* and *Lanius* are much alike and the similarity may indicate that they are related but this similarity alone does not constitute proof of relationship.

The patterns of *Chlorophoneus* and *Nilaus* (S-1986) are quite similar to one another and also to that of *Urolestes*. In *Urolestes* there are two faint bands visible in the middle of the pattern which seem to be absent in *Chlorophoneus* and *Nilaus*. This apparent absence could be due to loss of these minor fractions caused by denaturation of the samples. If so, the patterns of *Chlorophoneus*, *Nilaus* and *Urolestes* are nearly identical. Fresh specimens are needed to resolve

this question. The egg-white pattern of *Nilaus* differs from that of *Muscicapa* in having slower conalbumins and a faster ovalbumin region.

The egg-white pattern of *Laniarius* differs in several respects from those of *Lanius* but it has some aspects in common with that of *Urolestes*, including strong bands in the middle of the pattern where *Urolestes* has two faint bands. The two patterns also differ in several regions so no conclusions can be drawn from this comparison.

FAMILY PRIONOPIDAE, Woodshrikes. 0/14.

Sharpe (1877, 1903) created the family Prionopidae to accommodate twenty genera which he could not readily assign to other families. Mayr (1943) questioned this arrangement and re-assigned 17 of the genera, leaving only *Prionops*, *Sigmodus* and *Eurocephalus* in the Prionopidae. I have been unable to obtain egg-white specimens from any of these three genera.

Of the twenty original genera egg white is available only from *Grallina* (Grallinidae); *Colluricincla* (Muscicapidae) and *Nilaus* (Laniidae). Mayr (1943) placed *Nilaus* in the Muscipidae because it is "amazingly similar to *Batis*" except for the shrike-like bill. As noted under the Laniidae, the egg-white pattern of *Nilaus* is similar to that of *Chlorophoneus* and differs from that of the typical muscipids.

FAMILY CYCLARHIDAE, Peppershrikes. 1/2.

Species examined: *Cyclarhis gujanensis*

FAMILY VIREOLANIIDAE, Shrike-vireos. 1/3.

Species examined: *Vireolanius melitophrys*

Specimens of egg white from *Cyclarhis* and *Vireolanius* have been examined but the electrophoretic patterns, apparently due to excessive denaturation of the material, are unsuitable for critical comparisons.

Ridgway (1904) and Mayr and Amadon (1951) included *Cyclarhis* in the Vireonidae but Wetmore (1951, 1960) favored family status for the genus based upon Pycraft (1907). Mayr and Amadon (1951) also included *Vireolanius* in the Vireonidae based upon Zimmer (1942). Wetmore (1960: 20) retained the family Vireolaniidae on the basis of Pycraft's (1907) and his own studies of the pterylosis of the group.

FAMILY STURNIDAE, Starlings. 10/103, fig. 20.

Species examined: *Sturnus vulgaris*, *unicolor*; *Acridotheres tristis*, *fuscus*; *Spreo superba*, *bicolor*; *Aplonis panayensis*; *Lamprotornis purpureus*; *Onycognathus morio*; *Sturnia sturnina*.

Amadon (1943, 1956) has reviewed the genera of starlings and has speculated about their relationships to other passerine groups. As possible relatives Amadon (1956: 9) mentioned the Oriolidae, Vangidae, and Dicruiridae as the most likely candidates with the Prionopidae (including *Pityriasis*), Cracticidae, Paradisidae and Corvidae as possible but less likely allies. Amadon also discussed a possible sturnid-ploceid relationship and speculated that *Bubalornis*

and *Passer* might link the Sturnidae and Ploceinae, as von Boetticher (1931) had suggested. All of Amadon's remarks concerning these possible alliances were presented in a highly tentative fashion.

Sharpe (1890: 1) believed that the starlings "are undoubtedly allied" to the Corvidae and that the Artamidae "may be a Sturnine family." Stonor (1938) thought the pterylosis of the Paradiseidae indicates a relationship with the Corvidae, the Sturnidae, the Huia (Callaeidae) and *Picathartes* but not with the bower birds. Bock (1963), from a study of the skull, concluded that the birds of paradise and bower birds are related to one another and possibly derived from the Sturnidae. Lowe (1938) concluded that *Picathartes* and *Buphagus* are both starlings. Miller (1941) studied the myology of *Fregilupus varius* and concluded that it is a starling. Mayr and Amadon (1951) agreed with this allocation but Berger (1957) tentatively concluded from a study of its pterylosis, osteology and myology that it is not a starling. Berger (1957: 270) states that Amadon and Mayr "have both suggested a possible relationship between *Fregilupus* and the Prionopidae." Beecher (1953) considered the Sturnidae to be related to the sylviids, muscicapids and hirundinids. Most genera of starlings have a double humeral fossa (Bock, 1962b) and the Sturnidae is one of the families in which "Process D" is present on the carpometacarpus (Pocock, 1966). This condition agrees with Pocock's "passeroid" group which includes *Passer* and the Ploceidae, but not with the "lanioid" group which includes *Dicrurus*, *Corvus* and *Lanius*.

The egg-white patterns of *Sturnus* and *Lamprotornis* seem to differ from one another in that *Sturnus* has a separate "ovomucoid" region (Type B) whereas *Lamprotornis* shows but a single fast fraction (Type A). *Sturnus unicolor* and *Lamprotornis purpureus* have ovalbumins of the same mobility and it is probable that the apparent difference is due to the "ovomucoid" in *Lamprotornis* having a slightly greater mobility than in *Sturnus* and thus it appears to merge with the ovalbumin. However, the cathodally migrating hemoglobins of *Sturnus vulgaris* and *Lamprotornis nitens* differ in mobility and thus reinforce the possibility that these two genera may not be closely related (Sibley et al., in prep.).

The egg-white pattern of *Sturnus* is an especially good match for that of *Artamus* as discussed above under the Artamidae. (See gel # S-2386). An alliance between these two groups is possible and additional evidence should be sought. The patterns of other Type B groups also resemble that of *Sturnus* to varying degrees. Among these are *Pycnonotus*, *Dicrurus*, the Cracticidae, *Diphyllodes*, and even *Sitta*, the Ploceidae and the Turdidae. The pattern of *Promerops*, discussed under the Meliphagidae, also resembles that of *Sturnus*. The Corvidae, Sylviidae, Muscicapidae and Hirundinidae have patterns unlike those of the Sturnidae.

The egg-white evidence thus supports some of the previous proposals and disagrees with others. The most likely relatives of the starlings seem to be the Artamidae, Pycnonotidae and Dicruridae but several other groups are not ruled out. If *Promerops* was derived from the Sturnidae further evidence of relationship can be expected to emerge.

FAMILY MELIPHAGIDAE, Honey-eaters. 17/160, fig. 21.

Species examined: *Lichmera indistincta*; *Certhionyx variegatus*; *Myzomela sanguinolenta*; *Meliphaga fusca*, *chrysops*, *virescens*, *penicillata*, *ornata*, *leucotis*; *Melithreptus gularis*; *Phylidonyris pyrrhoptera*, *albifrons*, *melanops*, *novae-hollandiae*; *Xanthomyza phrygia*; *Manorhina melanoccephala*; *Promerops cafer*.

The honey-eaters are a large and diverse assemblage primarily confined to Australia, New Guinea and the islands of the southwest Pacific. The South African genus *Promerops* is placed in the Meliphagidae by some authors but others consider it only convergently similar to them.

The Meliphagidae are mainly nectar feeders and the brush-tipped tongue with the tip split into four divisions, each of which is frayed along one margin, is considered to be the diagnostic character of the family. The tongues of nectar-feeding birds have been studied by Gadow (1891), Gardner (1925), Scharnke (1931, 1932), Amadon (1950b), Dorst (1952) and Rand (1961, 1967). Gardner (1925) concluded that the structure of the tongue is of little taxonomic value in most groups but that in some, including the Meliphagidae and the Nectariniidae, it can be used to delimit a family. There is obviously the danger of circularity in this reasoning but these two families have been so defined for a long time. Scharnke (1932: 119 and 135) concluded that the tongue of *Promerops* is only convergently similar to that of the Meliphagidae and that the Meliphagidae, Promeropidae and Nectariniidae should be retained as separate families. Dorst (1952: 192) agreed with Scharnke that *Promerops* is not a meliphagid. Rand (1967) reviewed the variation in the tongues of nectar-feeding passerines and concluded that adaptation to nectar feeding has arisen in at least eight separate groups. Rand (1967: 58) pointed out that the tongue of *Promerops* differs from that of any of the Meliphagidae he has examined or seen illustrated. Rand notes that in *Promerops*, in contrast to the meliphagids, "only the two outer parts of the tip are frayed to give the brush tip. The two centered elements are not frayed and appear as if modified for probing." Mayr and Amadon (1951: 27) left *Promerops* in the Meliphagidae but noted "that its similarity may, after all, be parallelism."

Salomonsen (1933, 1964) has been the principal proponent of the opinion that *Promerops* is a meliphagid. He has based this conclusion upon the similarities in the tongue, alimentary canal, feeding habits, plumage pattern, and nest and eggs. Delacour (1944) agreed with Salomonsen concerning *Promerops*. Beecher (1953) also concluded that *Promerops* is a meliphagid and that other possible relatives of the Meliphagidae include *Aegithina* and the Estrildidae. Beecher (1953: 303) also proposed that "the Ploceidae arose from the Promeropinae or Cisticolinae in Africa."

Except for the *Promerops* problem the relationships of the Meliphagidae to other groups have produced little debate. They are usually compared with the other Old World nectar-feeders, particularly the Nectariniidae, Dicaeidae and Zosteropidae, but their closest relatives remain uncertain. Delacour (1944) expressed the opinion that the Meliphagidae are not especially close to the other nectar-feeding groups and Mayr and Amadon (1947) decided that the evidence linking the Meliphagidae, Nectariniidae, Zosteropidae and Dicaeidae is slight.

In 1951 Mayr and Amadon concluded that the Meliphagidae may be distantly related to the Dicaeidae. Dorst (1952: 212) concluded that the Meliphagidae is a heterogeneous group "sans nul doute artificiel."

The egg-white protein patterns introduce some additional complications and raise some new questions. Within the Meliphagidae there are at least two types of egg-white patterns. In *Meliphaga*, *Phylidonyris* and *Xanthomyza* the pattern is Type A with no clearly separate "ovomuroid" and relatively fast conalbumins. In *Lichmera*, *Certhionyx* and *Meliornis* (see gels #S-2389 and 2451) the pattern is Type B with a distinct ovomuroid and relatively slower conalbumins. The mobilities of component 18 and the ovalbumin region are the same in both pattern types. *Promerops* is discussed below. The patterns of the other available genera are not good enough to be defined with confidence.

These two pattern types may reflect the same situation noted in *Prinia* and several other groups. The "ovomuroid" fraction in the *Meliphaga* type of pattern is possibly present but migrating at nearly the same speed as the ovalbumin region and hence merges with it. In some patterns of *Meliphaga* and *Phylidonyris* a faintly separated fraction can be seen in the same relative position as the "ovomuroid" of *Lichmera*. However, the mobility differences of the conalbumins and the "ovomuroid" do constitute real and apparently consistent differences between the two types of patterns. Whether or not these two pattern types are correlated with natural subgroups within the Meliphagidae is not known but should be considered.

The *Meliphaga* type of pattern is similar to that of *Zosterops* but there are differences between them in the mobilities of the conalbumins and the ovalbumin region, both being slower in *Zosterops*. The *Meliphaga* type of pattern also resembles those of the sylviids, muscicapids, fringillids and other Type A groups.

The *Lichmera* type of pattern is like that of the Nectariniidae, Ploceidae and other Type B groups in having an "ovomuroid" clearly visible. There are apparently consistent mobility differences between them in the conalbumins and ovalbumins.

The pattern of *Pardalotus* is similar to those of *Lichmera* and *Certhionyx*, differing in the slower mobility of component 18 and slightly faster conalbumins and ovalbumin. The similarity between the patterns of *Pardalotus* and *Lichmera* suggests that *Pardalotus* may be related to the Type B honeyeaters and additional evidence should be sought. The pattern of *Acanthiza*, discussed under the Sylviidae, also resembles those of *Lichmera*, *Certhionyx* and *Pardalotus*.

The available patterns of *Promerops* are fairly good. They differ from the *Meliphaga* type of pattern in having a visible "ovomuroid" and conalbumins that migrate just ahead of component 18. Also, *Promerops* apparently lacks the strong pre-albumin which is seen in all meliphagid patterns. *Promerops* differs from the *Lichmera* type of meliphagid pattern in the slow mobility of its conalbumins and the lack of a pre-albumin. The *Promerops* pattern is similar to that of *Sturnus* and also to that of *Pycnonotus*. It differs from both in the mobilities of some fractions. The pattern of *Promerops* resembles that of *Nectarinia* in having a visible "ovomuroid" but, in detail, seems more like that of *Sturnus* than that of *Nectarinia*. In either case the similarities and differences are difficult to evaluate.

No conclusions are possible from the available evidence which poses several questions that merit additional study. These questions are:

- 1) Are there two (or more) groups of the Meliphagidae correlated with the *Meliphaga* and *Lichmera* pattern types?
- 2) Is *Pardalotus* related more closely to the group of meliphagids that includes *Lichmera* and *Certhionyx* than to *Dicaeum*?
- 3) Is *Acanthiza* related to *Lichmera* and *Pardalotus*, rather than to the Sylviidae?
- 4) Is *Promerops* most closely related to the Sturnidae, the Pycnonotidae, the Nectariniidae, the Meliphagidae or some other group?
- 5) Are the resemblances among the patterns of the Nectariniidae, Ploceidae, *Lichmera*, *Certhionyx*, *Pardalotus* and other groups with similar Type B patterns due to close genetic relationship?

FAMILY NECTARINIDAE, Sunbirds. 12/104, fig. 21.

Species examined: *Anthreptes malacensis*, *collaris*; *Nectarinia bouvieri*, *erythrocerca*, *jugularis*, *afra*, *famosa*, *talatala*, *senegalensis*, *olivacea*, *violacea*, *nectarinoidea*.

Delacour (1944) considered the sunbirds to be a compact, well-characterized group with natural affinities to the Dicaeidae and through them to *Remiz* and *Aegithalos*. Delacour also noted (p. 19) that the Zosteropidae "likewise resemble the sunbirds, though less markedly." Mayr and Amadon (1947) discussed the possible relationships of the several Old World nectar-feeding families and, although agreeing with Delacour that the sunbirds and flowerpeckers may be related, declined to render a strong opinion. Mayr and Amadon (1951: 25) stated that the "sunbirds, a very compact group (Delacour, 1944), are evidently relatives of the Dicaeidae." Beecher (1953) placed the sunbirds near the flowerpeckers and white-eyes and derived all three from the Pycnonotinae of his Sylviidae.

The egg-white patterns of the available sunbirds are essentially identical to one another. They differ from those of the *Meliphaga* type of honeyeater pattern but are similar to the *Lichmera* type. The pattern of *Pardalotus*, which resembles that of *Lichmera*, is also similar to that of the sunbirds although differing in several details.

The Type A patterns of *Zosterops* and *Aegithalos* are unlike the Type B patterns of the sunbirds and do not suggest a relationship with them. In gel #S-2281 the pattern of *Nectarinia* is similar to those of the bulbuls *Pycnonotus* and *Phyllastrephus*.

These observations do not provide a basis for any strong opinions about the relationships of the Nectariniidae but they suggest that the sylviids, *Aegithalos* and *Zosterops*, are probably not close relatives of the sunbirds while the bulbuls, some meliphagids, *Pardalotus* and perhaps other Type B groups could be.

FAMILY DICAEDAE, Flowerpeckers. 4/51, fig. 22.

Species examined: *Dicaeum geelvinkianum*, *hirundinaceum*; *Pardalotus ornatus*, *rubricatus*.

Mayr and Amadon (1947: 3) noted that the Meliphagidae, Nectariniidae and Zosteropidae "are often thought to be related to the Dicaeidae, but the evidence is rather slight." These authors also noted the many differences in structure and habits between the typical flowerpeckers (*Dicaeum*, *Anaimos*, *Rhamphocharis*, *Melanocharis*) and the pardalotes (*Pardalotus*, *Oreocharis*, *Paramythia*), which they considered as "aberrant genera" only distantly related to the typical dicaeids. In 1951 Mayr and Amadon (p. 25) noted that the dicaeid genus *Melanocharis* resembles certain meliphagids although "this resemblance may not indicate affinity." These authors also considered as a case of "moot affinity" a possible relationship between flowerpeckers and *Remiz* and noted certain resemblances between flowerpeckers and the Bombycillidae "in appearance, fondness for mistletoe berries, gregarious habits, and other details of behavior." Mayr and Amadon (1951: 25) also stated that the sunbirds "are evidently relatives of the Dicaeidae" thus following Delacour (1944). In all recent classifications the Dicaeidae appear next to the Nectariniidae and close to the other Old World nectar feeders (Mayr and Amadon, 1951; Mayr and Greenway, 1956; Amadon, 1957; Delacour and Vaurie, 1957; Wetmore, 1960).

The egg-white protein pattern of *Pardalotus rubricatus* has been discussed above under the Meliphagidae. It resembles the patterns of *Lichmera* and *Certhionyx* and thus raises the question of a possible relationship between *Pardalotus* and at least some genera assigned to the Meliphagidae. The similarity between the patterns of *Pardalotus* and *Acanthiza* is also discussed under the Sylviidae and the Meliphagidae.

The available patterns of *Dicaeum* are relatively poor but, in both disc and starch gel systems, it is possible to see differences between the patterns of *Pardalotus* and *Dicaeum*. However, until fresh, undenatured *Dicaeum* egg white can be examined, it is impossible to determine the extent of the differences.

These observations suggest, 1) that *Pardalotus* may be related to those honeyeaters with similar patterns such as *Lichmera* and *Certhionyx*, and 2) that *Pardalotus* and *Dicaeum* may not be closely related. Both suggestions are tentative and should be tested using other techniques.

FAMILY ZOSTEROPIDAE, White-eyes. 4/80, fig. 22.

Species examined: *Zosterops pallida*, *senegalensis*, *virens*, *palpebrosa*.

The Zosteropidae are small, nine-primaried oscines with slender, usually straight or slightly decurved bills, operculate nostrils and a bifid, protractile tongue each half of which is lacinate in many species. The wings are short, the tail short and square. The tarsus has a few scales in front and the outer toes are partially united. The plumage tends to be yellowish or greenish above and whitish, brownish or gray below. Most species have a circumorbital ring of small white feathers. The sexes are alike. The 80 species occur from Africa to Asia and Australasia.

As the above description indicates the members of this group tend to be relatively nondescript. The brush-tipped tongue has been the basis for placing them in the vicinity of the Old World nectar feeders although the nine-primaried wing and general appearance caused early systematists (e.g., Gray, Sundevall)

to place them near the wood-warblers (Parulini). Because the Dicaeidae have a small or vestigial tenth primary and, in some genera, a tongue adapted for nectar feeding, the white-eyes and the flowerpeckers are often assumed to be related. However, as noted by Mayr and Amadon (1951: 27), "the relationships of *Zosterops* remain to be discovered." Delacour (1944: 19) stated that "the Zosteropidae . . . resemble the sunbirds" but whether or not this implies that he believes that the sunbirds are the closest relatives of *Zosterops* is uncertain. Beecher (1953) interpreted his jaw muscle data as indicating that *Zosterops* was derived from the bulbuls (Sylviidae: Pycnonotinae) and related to the Nectariniidae and Dicaeidae.

The available egg-white patterns of *Zosterops* are unlike those of the Nectariniidae, Pycnonotidae and Dicaeidae (*Dicaeum* and *Pardalotus*) in both starch and "disc" gel electrophoresis. In both systems *Zosterops* shows a relatively simple Type A pattern consisting of a compact ovalbumin region with no evidence of an "ovomuroid" fraction. These characters distinguish *Zosterops* from the Old World nectar-feeders except those Meliphagidae with Type A patterns (e.g., *Meliphaga*).

In gel S-2281 the pattern of *Zosterops* is similar to that of *Muscicapa* differing only in the mobility of the ovalbumin which is faster in *Muscicapa*. The similarity to *Muscicapa* means that the *Zosterops* pattern is also similar to that of the Sylviidae, Fringillidae and other groups with Type A patterns. Some patterns of the cardueline finches are virtually identical to that of *Zosterops*.

Thus, although these observations cannot be considered conclusive, the egg-white evidence suggests that the closest relatives of *Zosterops* may be the sylviid-muscicapid assemblage and that the dicaeids and nectariniids are probably not close relatives.

FAMILY PLOCEIDAE, Weaverbirds, Waxbills, Grassfinches, Mannikins. 60/219.

SUBFAMILY BUBALORNITHINAE, Buffalo-weavers, 1/3, fig. 22.

Species examined: *Bubalornis albirostris*.

SUBFAMILY PLOCEINAE, Typical weavers. 30/109, figs. 22, 23.

Species examined: *Amblyospiza albifrons*; *Ploceus baglafecht*, *ocularis*, *melanogaster*, *capensis*, *subaureus*, *xanthops*, *xanthopterus*, *castanops*, *intermedius*, *velatus*, *spekei*, *cucullatus*, *melanocephalus*, *jacksoni*, *superciliosus*, *benghalensis*, *manyar*, *philippinus*, *megarhynchus*; *Malimbus nitens*; *Quelea cardinalis*, *quelea*; *Euplectes afer*, *orix*, *axillaris*, *albonotatus*, *ardens*, *progne*; *Spermophaga ruficapilla*.

SUBFAMILY ESTRILDINAE, Waxbills, Grassfinches, Mannikins. 29/107, fig. 23.

Species examined: *Nigrita bicolor*; *Pytilia afra*; *Estrilda senegala*, *rubricata*, *astrild*, *coerulescens*, *angolensis*, *temporalis*, *melanotis*, *amandava*, *subflava*; *Oritospiza atricollis*; *Zonaeginthus pictus*, *guttatus*; *Poephila phaeton*, *modesta*, *guttata*, *bichenovi*; *Padda oryzivora*; *Amadina fasciata*, *erythrocephala*; *Lonchura malabarica*, *fringilloides*, *cucullata*, *molucca*, *striata*, *punctulata*, *maja*, *castaneothorax*.

INCERTAE SEDIS

SUBFAMILY VIDUINAE, Widow-birds. 4/9, fig. 24.

Species examined: *Vidua macroura*, *chalybeata*, *paradisaea*, *funerea*.

FAMILY PASSERIDAE, Sparrow-weavers.

SUBFAMILY PASSERINAE, Sparrow-weavers. 11/35, fig. 24.

Species examined: *Histurgops ruficauda*; *Philetairus socius*; *Passer domesticus*, *hispaniolensis*, *melanurus*, *montanus*, *luteus*; *Petronia superciliaris*; *Montifringilla nivalis*; *Plocepasser mahali*; *Pseudonigrita arnaudi*.

"The classification of the thick-billed, seed-eating passerines and their allies has been and is one of the most controversial aspects of avian systematics today." Following this understated introduction Winterbottom (1966) reviewed a number of recent arrangements which have been proposed for the thick-billed passerines and concluded with an appeal to "stick to the traditional classification until greater agreement has been reached."

The arguments concerning the relationships of the various weavers and other thick-billed passerines revolve primarily around the following questions:

- 1) Should the ploceines and estrildines be included in a single family or treated as two separate families?
- 2) Are the estrildines related more closely to the ploceines or to the carduelines?
- 3) Is *Passer* more closely related to the ploceines and estrildines, to the fringillids, or to some other group?
- 4) Should a family Passeridae be recognized and is it true that *Montifringilla*, *Petronia* and *Pyrgilauda* are closely related to *Passer*, as proposed by Sushkin (1927)?
- 5) Are the widow-birds (*Vidua*) related most closely to the ploceines, the estrildines or to some other group?
- 6) What are the closest relatives of such genera as *Bubalornis*, *Philetairus*, *Pholidornis*, *Plocepasser* and *Sporopipes*?

The recent history of the classification of the weaverbirds begins with Chapin (1917) who reviewed previous proposals and examined the characters used to classify these groups. Chapin emphasized that the size of the outer (tenth) primary was misleading as the basis for subdividing the weavers and he introduced the presence of mouth-markings in the nestlings to define the estrildines. Chapin noted that the ploceines, estrildines, *Passer*, *Pinicola* and *Paroaria* are essentially alike in skeletal characters but that *Bubalornis* (*Textor* of Chapin) differs from all of these in both cranial and sternal characters. Chapin separated the buffalo-weavers (*Bubalornis*, *Dinemellia*) as a family on the basis of their unusual nesting habits, extremely long tenth primary, spotted eggs, lack of mouth-markings in nestlings, tarsal scutellation, and the presence of the unique phalloid organ in *Bubalornis*. Chapin placed the ploceines and estrildines in a single family, Ploceidae. He included the widow-birds and *Pholidornis* in the Estrildinae and placed *Sporopipes*, *Histurgops*, *Plocepasser* and *Philetairus* in the Ploceinae.

Sushkin published two preliminary papers (1925 a and b) and a more complete treatment (1927) of his studies on the anatomy and classification of the weaverbirds. He concluded (1927) that *Passer*, *Petronia*, *Montifringilla*, *Pyrgilauda*, *Gymnoris*, *Onychostruthus* and *Sorella* are related to one another and should constitute a subfamily, Passerinae, in the Ploceidae. Characters allying these genera to one another as cited by Sushkin included: skeletal structure, similarities in the palatal surface of the rhamphotheca, a complete post-juvenal molt, and nest structure.

Sushkin relied heavily upon the configuration of the ridges and furrows visible on the palatal surface of the horny bill sheath but he also compared the tarsal scutellation and several skeletal elements. The unique characters of *Bubalornis* were recognized by Sushkin but he chose to employ a single family, Ploceidae, and to include within it the subfamilies Bubalornithinae, Plocepasserinae (including *Plocepasser*, *Pseudonigrita*, *Histurgops*, *Philetairus*), Passerinae, Sporopipinae, Estrildinae and Ploceinae.

Sushkin (1927: 23) suggested that some characters of *Phytotoma* "may seem to entitle [it] to an ancestral relation to *Bubalornis*" but he also noted that these two genera differ in many ways. The Passerinae were considered by Sushkin to be nearer to the Ploceinae than to the Estrildinae, *Vidua* to be closer to the Estrildinae than to the Ploceinae, and *Sporopipes* closer to the ploceines and estrildines than to the Passerinae.

Chapin (1929) responded to the papers by Neunzig (1928, 1929) with a vigorous reaffirmation of his belief that the viduines are closely related to the estrildines and that *Pyromelana* and *Coliuspasser* are ploceine and not close to *Vidua*, as suggested by Neunzig. In this paper Chapin reported (p. 482) that *Vidua*, unlike most passerines, has a row of lesser upper secondary coverts. Morlion (1964) reported *two* rows of these coverts in *Vidua* and Zeidler (1966: 123 and fig. 17) found an apparently homologous row of seven small, downy feathers in *Passer*. In an attempt to resolve this question I wrote to Prof. E. Stresemann in December, 1967 and again in January, 1968. Prof. Stresemann's replies and summaries of the statements from the papers of Chapin, Morlion and Zeidler are presented in Table 1.

As noted by Stresemann in his letter of December 14, 1967, the Viduinae differ from all of the other groups in Table 1 in having the lesser upper secondary coverts well developed, as originally noted by W. de W. Miller in Chapin (1929). *Passer* also has a single row, but they are small and downy. In *Ploceus* there are *two* rows, one of which may be marginal coverts, but in the estrildines there is no sign of the lesser upper secondary coverts.

It is difficult to draw any firm conclusions from the above. Each group differs from the others and the assignment of homologies is uncertain. *Vidua* seems to be most like *Passer* and least like the Estrildinae in this character. However, in the absence of information concerning the functional significance of the different degrees of development of the lesser upper secondary coverts it is impossible to interpret their taxonomic value.

Chapin (1929: 482-3) also noted that *Vidua* differs from the estrildines and from most ploceines in having a first lower greater primary covert as do most oscines. *Passer* also has this covert (Zeidler, 1966: fig. 10).

TABLE I Lesser Upper Secondary Coverts

Author	Group	Condition
Chapin, 1929	Viduinae	One row of well-developed feathers. <i>V. macroura</i> has a "normal" row; <i>V. paradisaea</i> and <i>V. fischeri</i> have five good-sized lesser coverts, the distal two or three being absent; <i>V. ultramarina</i> has six.
Morlion, 1964	Viduinae	"Contrary to <i>Textor</i> and <i>Estrilda</i> , <i>Hypochera</i> [= <i>Vidua</i>] has two incomplete rows of well-developed quills as upper lesser secondary coverts. They are standing in the place of the double row of downy feathers in <i>Textor</i> ." (p. 142)
Stresemann, letter dated Dec. 14, 1967	Viduinae	In <i>V. chalybeata amauropteryx</i> and <i>V. regia</i> there is one row of five <i>well-developed</i> feathers, representing numbers 3 to 7. The distal feathers 1 and 2 are lacking altogether.
Stresemann, letter dated Jan. 18, 1968	Viduinae	In <i>V. regia</i> and <i>V. ultramarina</i> there is only <i>one</i> row of well-developed lesser upper secondary coverts. "This is the result of the <i>second</i> careful inspection."
Chapin, 1929	<i>Passer</i>	No comment.
Morlion, 1964	<i>Passer</i>	No comment.
Zeidler, 1966	<i>Passer</i>	One row of seven small, downy feathers.
Stresemann, letter dated Dec. 14, 1967	<i>Passer</i>	Seven small, downy feathers—personal inspection.
Chapin, 1929	Ploceinae	Lacking, but represented by downy vestiges in <i>Bubalornis</i> and <i>Dinemellia</i> .
Morlion, 1964	Ploceinae	According to text, p. 115, lacking; but fig. 3, p. 120 shows a double row of downy feathers in <i>P. nigerrimus</i> .
Stresemann, letter dated Dec. 14, 1967	Ploceinae	Represented by a double row of downy structures, (Morlion and personal inspection).
Stresemann, letter dated Jan. 18, 1968	Ploceinae	"In <i>Ploceus nigerrimus</i> there are <i>two</i> rows of downy feathers intercalated between tectrices mediae superiores and tectrices marginales. The row next to t. med. sup. shows a better development than the next one and represents the t. minores sup. The other row <i>may</i> belong to the t. marginales, but this assignment is a matter of opinion and not a verdict."
Chapin, 1929	Estrildinae	Lacking.
Morlion, 1964	Estrildinae	Lacking.
Stresemann, letter dated Dec. 14, 1967	Estrildinae	Lacking (fide Morlion).

Von Boetticher (1931) suggested that the Ploceidae and Sturnidae are related and that *Bubalornis* on the ploceid side and *Buphagus* on the sturnid side are the "primitive" members of their respective families and closest to one another. Von Boetticher also suggested that the nine-primaried oscines, including the Motacillidae, and the Dicaeidae, were derived from the ploceid-sturnid complex.

Delacour and Edmond-Blanc (1933-1934) revised *Euplectes* and *Vidua* and proposed that a separate subfamily, Viduinae, be recognized in the Ploceidae

for the widow-birds. Delacour (1943b) revised the Estrildinae and concluded that the nearest relatives of the estrildines are the Viduinae and that these groups have evolved from the Sporopipinae. Delacour also stated that he was (p. 73) "inclined to think that the Ploceidae are really nearer to the Sturnidae than to the Fringillidae" as indicated by their nesting habits. The starlings are hole-nesters and the weavers build a covered nest. Delacour suggested that these nest types are more similar to one another than either is to the usual open nest of fringillids. Delacour (1943b: 71) placed *Anomalospiza* in the Ploceinae and proposed that *Pholidornis* should be placed near *Hylia* in a family Hyliidae between the Zosteropidae and Nectariniidae, thus following Bates (1930). Paynter (1967: 208, footnote) has placed both *Hylia* and *Pholidornis* in the Sylviidae.

Fiedler (1951) interpreted his jaw muscle comparisons as indicating a relationship between the Fringillidae and Ploceidae but Beecher (1953) placed these two groups some distance apart. He found the Ploceidae, with subfamilies Ploceinae, Viduinae and Passerinae, to be quite different from the Estrildidae in jaw musculature. Beecher (p. 303) suggested that the Estrildidae may have "arisen from the Meliphaginae or Cisticolinae in Australia, while the Ploceidae arose from the Promeropinae or Cisticolinae in Africa."

Poulsen (1953) studied the behavior of viduines foraging on the ground. He found that they use "a kind of primitive scratching movement" with the feet which is not found in the ploceines or estrildines. These latter groups use only the bill and make pecking or shaking movements with the head to uncover seeds. In November, 1967, I wrote to Dr. Poulsen and asked him to compare the foraging behavior of *Passer* with that of the viduines and ploceids. In a letter dated January 26, 1968, Dr. Poulsen reported that he had now observed *Passer domesticus*, *P. montanus* and *P. flaveolus* when they were searching for food. All three species used the bill as do the ploceids, none used the scratching movements of the viduines. Dr. Poulsen further noted that the viduines scratch in the same manner as the emberizine genus *Junco*. The taxonomic significance of these observations is uncertain because, as reported by Harrison (1967), this "double scratch" movement is found primarily in birds that hop, such as the New World emberizine genera *Junco*, *Passerella*, *Pipilo*, etc., but not in those that walk, such as *Emberiza* and *Calcarius*.

Tordoff (1954a) concluded, primarily from a study of cranial and palatal characters, that the Carduelinae are allied to the Estrildinae. He included these groups as subfamilies in the Ploceidae along with the Bubalornithinae, Passerinae, Ploceinae and Viduinae. Stallcup (1954), from a study of pelvic musculature and a serological comparison of the saline-soluble proteins of the trunk muscles, heart, lungs and kidneys, concluded that the carduelines can be distinguished from the New World finches and tanagers and that, in the major features of leg musculature, the carduelines are like the ploceids. Stallcup also found the carduelines to be serologically distinguishable from the richmondenines, emberizines and tanagers. The carduelines, according to Stallcup (1954: 204), show more serological similarity to the estrildines than to the New World groups. In fact, according to Stallcup, the estrildines are serologically more like the New World groups than are the carduelines. Thus, as is frequently the case in serological

comparisons which use such a large array of antigens, Stallcup's data are ambiguous. Nevertheless he concluded that a family Carduelidae, containing the Estrildinae and Carduelinae, was justified, thus following Tordoff in part.

Chapin (1954: 286-8) returned to a treatment of the weavers more like that of Sushkin (1927) in which the Bubalornithinae were placed in the Ploceidae. Chapin expressed the opinion that the Viduinae are closest to the Estrildinae and not close to *Euplectes*.

Steiner (1955) stressed the many differences between the typical weavers (Ploceinae) and the waxbills (Estrildinae) and argued strongly for recognition of the latter as a separate family (Spermestidae). Wolters (1957), although concerned primarily with generic and specific limits, placed the Viduinae as a subfamily in the Estrildidae. Simmons (1957) noted that ploceines have been observed to "ant" but that estrildines seem not to do so.

Mainardi (1958) reviewed the conclusions of Beecher, Tordoff and Stallcup and added his own data from a serological comparison of red-cell antigens. Mainardi concluded that the Estrildinae and Passerinae are closely related and also that the Emberizinae are related most closely to *Fringilla*. Mainardi (1958: 336) stated that the "Carduelinae are intermediate between Estrildinae and Passerinae on one side, and Emberizinae and *Fringilla* on the other." Mainardi also presented some data on the paper electrophoretic patterns of the hemoglobins of these groups which he believed showed agreement with his serological data.

White and Moreau (1958) accepted family rank for the Estrildidae and discussed the subfamilies to be included in the Ploceidae. They found the arrangement which includes the Sporopipinae in the Ploceidae to be doubtful but (p. 141) "pending further studies of *Sporopipes* . . . we include it in the Ploceinae." Wolters (1966) placed *Sporopipes* closest to the Estrildinae.

Crook (1958) studied the behavior of *Bubalornis* and concluded that his data and anatomical characters supported family rank for the Bubalornithidae, although he had no information on the behavior of *Dinemellia*.

Steiner (1960) based a revision of the Spermestidae (= Estrildinae) primarily upon the mouth-markings of the nestlings and reaffirmed his belief that the group deserves family status. Steiner (p. 111) also discussed the relationships of the widow-birds and concluded that they are actually a subfamily of the Ploceidae and that their similarities to estrildines are due to mimicry of the host species, not to close relationship.

Friedmann (1960) reviewed all of the literature on the parasitic weavers and concluded that the widow-birds are most closely related to the estrildines and yet, because they possess a number of characters not shared with either ploceines or estrildines, they should be treated as a subfamily, Viduinae, in the Ploceidae. Friedmann (1960: 8) questioned whether or not there was a valid basis for keeping the Ploceidae distinct from the Fringillidae and noted that "In view of the general acceptance of the muscapine-sylviine-turdine assemblage in one family, it appears that a similar amalgamation may be justified here." Friedmann expressed the opinion that a consolidation of this type is more appropriate than to follow Steiner's suggestion that the estrildines be placed in a family separate from the other weavers.

Wolters (1960) placed the Viduinae as a subfamily of the Estrildidae while Nicolai (1961) found that the widow-birds had ploceid-like elements in their vocalizations. Friedmann (1962) published a critique of the papers by Steiner (1960), Wolters (1960) and Nicolai (1961) and defended his previous opinion (1960) that the viduines are closest to the estrildines and that both groups should be placed in the Ploceidae.

Collias and Collias (1964) studied the evolution of nest-building in the Ploceidae and concluded that their observations, as a rule, agreed with Chapin's (1917) classification. A diagram of relationships presented by Collias and Collias (1964: 116) "was arrived at after consultations with James P. Chapin and Herbert Friedmann." This diagram includes as subfamilies of the Ploceidae the Bubalornithinae, Passerinae, Plocepasserinae, Ploceinae, Sporopipinae, Estrildinae and Viduinae. The Passerinae and Sporopipinae are indicated as groups whose relationships are uncertain. The nests of the Passerinae "did not bear any close resemblance to those of any of the other subfamilies" (p. 118). The nests of the buffalo weavers are most like those of the Plocepasserinae, that of *Dinemellia* being similar to the nest of *Plocepasser mahali*, and the nests of the Ploceinae are also most like those of the Plocepasserinae. The nests of the estrildines vary greatly but are most similar to that of *Sporopipes*. Wolters (1966), as noted above, placed *Sporopipes* closest to the Estrildinae.

Crook (1964) has been concerned primarily with the behavior of the Ploceinae but he has presented a classification of the genera and species within the subfamily.

Nicolai (1964), following a long and detailed study of the breeding behavior of the Viduinae, concluded that (p. 201) "In their courtship, in the innate song elements, in the seasonal alteration of breeding plumage and cryptic dress, and in their plumage characters the Viduinae reveal themselves as close relatives of the Euplectinae, a subfamily of the weaverbirds (Ploceidae)."

Ziswiler (1964, 1965, 1967a) concluded from a comparative study of feeding behavior, the bill, skull, the jaw muscles and their innervation, the horny palate and the digestive tract that the Viduinae are related to the Ploceidae and are closest to the *Euplectes* group, thus agreeing with Nicolai (1964). Ziswiler proposed the division of the Ploceidae into a *Euplectes* group and a *Ploceus* group and supported the separation of the Estrildidae as a separate family, following Steiner. Moreau (1967) has pointed out that *Passer* dust-bathes but the Ploceinae do not, contrary to the reference in Ficken and Ficken (1966: 652).

Pocock (1966) compared certain small foramina in the posterior wall of the orbit of several groups of oscines. He found that the ploceines, estrildines, *Bubalornis*, *Plocepasser*, *Amblyospiza* and *Sporopipes* agree with one another in lacking the pair of "foramina G" which are present in *Passer*, *Petronia*, the carduelines and many other families of Passeres. Pocock suggested that these skull characters indicate that *Passer* is closer to the carduelines than to the Ploceidae or *Plocepasser* and that resemblances between *Passer* and the Ploceidae are due to convergence. He recommended that a family, Passeridae, be recognized. However, Pocock (1966: 94) quotes Bock as believing "that the minor skull foramina can change position quite easily during evolutionary processes and hence constitute a poor taxonomic criterion." Pocock agreed

with this opinion but held to one firm conclusion, namely, "that the Passeridae are less closely related to *Plocepasser* and the rest of the Ploceidae than usually believed and hence deserve family rank."

Pocock did not examine *Vidua* but I have done so and find, in two skulls of *V. macroura*, that the "foramina G" are absent but represented by a pair of shallow grooves, one on each side of the interorbital septum above the ridge of the cerebral fossa. This condition in *Vidua* agrees with that in some ploceines and in the swallow, *Riparia paludicola*, reported by Pocock (1966: 91). I have also confirmed Pocock's observations on these foramina in *Passer*, several estrildines, and several emberizines. Karl Tolonen (personal communication) extended this study by examining 120 skulls of passerines representing 20 families, many of them not included in Pocock's material. Tolonen found a considerable range of individual variation in the foramina. In *Junco*, for example, the variation included the conditions which Pocock thought could be used to separate *Passer* from the Ploceidae. Tolonen concluded that the foramina defined by Pocock actually exhibit a continuum and that they are of doubtful taxonomic value at any level.

Mainardi (1960) used the compilation of records of bird hybrids by Gray (1958) as the basis for calculating a "degree of affinity" between species of the families Fringillidae, Ploceidae, Thraupidae and Icteridae. One need only read the actual statements in Gray concerning the doubts expressed about the validity of some of the records to conclude that they constitute an unreliable basis for such an analysis. Although the records of hybrids between species in the same subfamily usually seem trustworthy there is considerable doubt about those between subfamilies and especially about records of hybrids between the Ploceidae and the Fringillidae. Until hybrid data which are above suspicion can be presented it seems best to omit them from consideration.

Ziswiler (1967b) compared the seed-opening mechanism, the horny palate and the alimentary canal of *Montifringilla nivalis* with these structures in other seed-eating oscines. He concluded that *Montifringilla* is most like the Ploceidae in these characters and should be placed with *Passer* in the Passerinae.

The egg-white protein patterns present us with some new and partly controversial data. First, it is clear that the Type B egg-white patterns of the Ploceinae are all like one another and those of the Estrildinae are like one another. Furthermore, the ploceine pattern agrees in all major features with the estrildine pattern although most estrildine patterns tend to be more spread out because the estrildine ovalbumin region tends to migrate faster and the conalbumin region slower than their counterparts in the ploceines. The egg-white data thus indicate that the ploceines and estrildines, though readily separable, are related to one another more closely than either is to any other group. To reduce the number of passerine families whenever the evidence indicates natural relationships is surely a reasonable procedure. I therefore advocate that the Estrildinae be treated as a subfamily of the Ploceidae in spite of the differences between them.

The allocation of *Bubalornis* can be handled in somewhat the same way. In addition to many anatomical differences *Bubalornis* egg-white patterns also differ somewhat from those of *Ploceus*. However, there is also an impressive

similarity between them in the ovalbumin region and component 18 has the same mobility in both. The main differences lie in the "ovomucoid" and conalbumin regions. These two regions are distinct and well separated in *Ploceus*. In *Bubalornis* they appear to have such similar mobilities that they have merged. This gives the two patterns a different appearance of uncertain significance. Those who wish to emphasize the differences can add the egg-white data to those characters which separate *Bubalornis* from the Ploceidae and argue for the recognition of a separate family Bubalornithidae. However, in spite of the differences between them it seems highly probable that *Bubalornis* is more closely related to the Ploceidae than to any other living group. A relationship between *Bubalornis* and the Sturnidae is not supported by the egg-white patterns nor by the hemoglobin patterns. The cathodally migrating hemoglobins of *Bubalornis* and *Buphagus* differ in mobility. Sushkin's (1927) suggestion that some characters of *Phytotoma* suggest a relationship to *Bubalornis* is not supported by the egg-white patterns.

Although recognizing that *Bubalornis* is a distinctive genus, not extremely close to the ploceines, I believe it is probably closer to them than to any other group. It therefore seems best to include the Bubalornithinae in the Ploceidae. It will be of particular interest to determine whether or not the egg-white protein pattern of *Dinemellia* is similar to that of *Bubalornis*.

The Type A egg-white patterns of the five available species of *Passer* are like one another and they differ strikingly from those of the ploceines and estrildines. In most aspects the pattern of *Passer* resembles that of the carduelines, emberizines, parulines and other "nine-primaried oscines" (= Fringillidae of this paper) but it differs in having a faster ovalbumin region and slower conalbumins. *Passer* is like the emberizines etc. in having an extremely slow component 18. Whether or not these similarities indicate relationship is uncertain. The hemoglobin patterns of *Passer*, the ploceines and the emberizines are all quite similar to one another and to several other groups. Thus they do not oppose a relationship between *Passer* and the nine-primaried oscines.

Another problem arises when *Passer* egg-white patterns are compared with those of *Philetairus* and *Montifringilla* which are considered by some authors to be related to *Passer*. The egg-white patterns of *Philetairus* and *Passer* are possibly more similar to one another than either is to the Ploceidae but they also differ in several respects. *Philetairus* shows an unusual series of at least three pre-albumin bands, *Passer* seems to have but one or two. The two genera also differ slightly in the ovalbumin region but they are more alike in the remainder of the pattern. The question thus remains open. *Philetairus* may be closer to *Passer* than to the ploceines or other groups but it seems to be well-marked and the degree of its relationship to *Passer* remains to be determined.

Montifringilla is even less satisfactory than *Philetairus* as a relative of *Passer*. The two differ in all parts of their egg-white patterns and that of *Montifringilla* is a better match for that of *Ploceus* than for the pattern of *Passer*. *Montifringilla* is not similar to the emberizines, carduelines, parulines or other nine-primaried oscines in its egg-white pattern. The original suggestion by Sushkin (1925a: 37) that the Passerinae should include *Passer*, *Gymnorhis*, *Petronia*, *Pyrgilauda* and *Montifringilla* was based upon "peculiarities of anatomo-

mical structure . . . moulting of the juvenile quills and tail-feathers in the first autumn, as well as in the construction of dome-shaped nests." In the same paper Sushkin discussed the affinities of the emberizines, tanagers, icterines, carduelines, cardinals, parulines, etc. With reference to the wood warblers (Parulidae = Mnioiltidae) Sushkin stated that they (p. 38) "have nothing to do with the whole assemblage." His "assemblage" in this case included the Icteridae, Coerebidae, Thraupidae (Tanagridae), Emberizidae, Fringillidae, Ploceidae and Drepanididae. Some of Sushkin's conclusions are still acceptable but no one today can seriously question the close alliance between the Parulidae and the other New World nine-primaried oscines. Since Sushkin's evidence led him so far astray in this case it is difficult to know how much credence to place in his other conclusions. Some of them, for example an alliance between the carduelines and drepanids, are supported by more recent studies but several other aspects of the arrangements proposed by Sushkin (1925a: 38) are no longer tenable. In his later paper Sushkin (1927: 1) stated that "on examination of the skeletons I have found that the genera *Passer*, *Petronia*, *Chionospina* [= *Montifringilla*] and *Pyrgilauda* are most intimately related. Besides the skeletal structure, they have in common certain characters of the external anatomy: in the first place, the very characteristic relief of the palatal surface of the horny bill . . . ; a total molt . . . of the young bird in the first autumn; the architecture of the nest, which is always domed with a side entrance, if built free, or placed in an enclosed space and thus also covered."

These characters seem like an uncertain basis for the proposed subfamily. Sushkin did not specify the nature of the skeletal evidence although (1925a: 37) he mentions the bony palate. In the 1927 paper Sushkin compared many of the skeletal elements of *Passer* with those of *Bubalornis*, *Plocepasser* and other genera but *Montifringilla* is not mentioned. Bock (1960) has cast doubt on some aspects of the bony palate as a source of valid taxonomic characters in the passerines, particularly the palatine process of the premaxilla. If, as seems probable, Sushkin based his claim of palatal similarity between *Passer* and *Montifringilla* on the palatine process of the premaxilla (= "palato-maxillaries" of many authors, *vide* Bock, 1960: 371-375) it is appropriate to note that Bock (1960: 470), after an exhaustive study of this structure in the Passeres, concluded that it "has *little or no* value in showing relationships between families of passerine birds or in placing problem genera in the correct family." The palatal surface of the rhamphotheca was used extensively by Sushkin as a character to delineate subgroups of the thick-billed passerines. He was impressively successful in determining the boundaries of the Carduelinae, for instance. Sushkin used this same character as the basis for the classification proposed in his 1925a paper in which the Fringillinae, Cardinalinae, Carduelinae and Drepanididae are placed in a separate Superfamily, Fringilloidei, from the Emberizoidei to which Sushkin assigned the Icteridae, Coerebidae, Tanagridae and Emberizidae—and left the Parulidae out altogether. As will be noted below, the egg-white protein evidence agrees with this arrangement in part although the paruline warblers are also clearly related to this assemblage.

The possession of similar nests can as easily result from convergence as from common ancestry and, moreover, as Collias and Collias (1964) noted, the

nests of *Passer* are quite unlike those of the typical Ploceidae. A complete post-juvenal molt is also found in many larks and swallows, in some fringillids (*Carpodacus mexicanus*, *Cardinalis cardinalis*, *Emberiza calandra*, *Ammodramus saviannarum*, *Melospiza melodia*), some icterids (*Sturnella magna*, *Molothrus ater*, *Agelaius phoeniceus*) and in *Aegithalos*, *Psaltiriparus*, *Panurus*, *Sturnus* and others. Other species in these groups have an incomplete post-juvenal molt and the extent of this molt varies in different individuals of some species (Dwight, 1900; Witherby et al., 1938; Ingram, 1955; Stresemann and Stresemann, 1966). Thus the characters supposedly linking *Passer*, *Montifringilla*, etc. as proposed by Sushkin are of quite uncertain value. The egg-white evidence suggests that *Passer* and *Montifringilla* are not closely related and that *Passer* may be closer to the Emberizinae while *Montifringilla* may be closer to the Ploceinae. Ziswiler (1967b) has reviewed the taxonomic position of *Montifringilla* and has studied the bill, rhamphotheca and alimentary tract. He concluded that *Montifringilla* is ploceine but he considers *Passer* also to be ploceine.

In view of the conflicting evidence concerning the relationships of *Passer* it seems appropriate to re-open the question and to seek additional data.

The egg-white patterns of the widow-birds (Viduiinae) produce further surprises. Because of the impressive similarity of the patterns of the species of the Ploceinae and Estrildinae to one another and because these two groups have been the only ones seriously considered to be related to the Viduiinae, I had expected that the egg-white patterns of the widow-birds would resemble those of the Ploceidae. The first specimen of *Vidua* egg white was sent to me by Dr. J. Nicolai and was laid by a captive bird. When the egg-white pattern was examined and found to resemble that of *Passer* rather than that of the Ploceidae, I wrote to Dr. Nicolai and suggested that a mistake in identification might have been made. He thereupon collected another egg, under circumstances precluding that it could have been laid by a *Passer*, and sent the egg white to me. This too produced a pattern remarkably similar to that of *Passer* and unlike those of the Ploceidae. Other specimens, taken in the field, have given the same result. The Type A egg-white protein pattern of *Vidua*, in both starch gel and disc electrophoresis, is unlike the Type B ploceine-estrildine pattern and much like the pattern of *Passer*. As noted above, the pattern of *Passer* is similar to that of the nine-primaried oscines (Emberizinae, etc.) and that of *Vidua* is also. In disc gel electrophoresis the pattern of *Vidua* egg white is a good match for those of the carduelines, parulines, emberizines, etc. but differs from those of the Ploceidae. In starch gel the *Vidua* pattern is seen to differ from that of the nine-primaried oscines in having slightly faster ovalbumins and slower conalbumins. It thus resembles the *Passer* pattern somewhat better. These comparisons are readily seen in gels #435 and #661 in which the egg-white proteins of *Passer*, *Vidua*, *Lonchura*, *Poephila*, *Ploceus*, *Spizella*, *Agelaius* and *Cyanocompsa* were compared, side by side. The similarities between *Passer* and *Vidua* and the differences between *Vidua* and the ploceids are easily seen. *Vidua* and *Passer* differ in having slightly different mobilities for component 18 and the conalbumins and there is a small difference in the configuration of the ovalbumin region. *Vidua* differs from the ploceids in lacking the prominent "ovomucoid" fraction and in the mobilities of other components.

What then do these similarities and differences mean? Because most or all of the previous discussions of viduine relationships have considered only the ploceines, euplectines and estrildines as possible relatives it is now necessary to examine *Passer* as an additional candidate. In addition to the egg-white evidence *Vidua* agrees with *Passer*, and differs from the Ploceidae, in having a single, well-developed row of lesser upper secondary coverts (see Table I) and a first lower greater primary covert (Chapin, 1929; Zeidler, 1966). On the other hand several other lines of evidence have been interpreted as indicating that the viduines are related to the ploceids. Rather than attempting to discredit one set of data and to support the other it seems best simply to suggest that the problem is not yet settled. If *Vidua* is actually closer to *Passer* than to the Ploceidae, additional evidence will soon be found.³ The egg-white data do not prove a *Vidua*-*Passer* alliance but they do indicate that in future comparisons *Passer* must be considered along with the ploceids. At the very least the egg-white data suggest that the ploceines and estrildines may be closer to one another than either is to *Vidua*.

Various suggestions for a relationship between the Ploceidae and such groups as the Sturnidae (Delacour, 1943b; Amadon, 1956), Nectariniidae (Pocock, 1966), or the Meliphagidae, *Promerops* or *Cisticola* (Beecher, 1953) have been made. The patterns of *Sturnus* and the nectariniids do resemble one another and, since they have the "ovomucoid" fraction, they also resemble the ploceid pattern. However, such general similarities, in the absence of strong supporting evidence of other kinds, do not constitute proof of relationship. The hemoglobins of *Nectarinia* are quite unlike those of the ploceids in starch gel (Sibley et al., in prep.). Neither the hemoglobin nor egg-white patterns of *Cisticola* are similar to those of the Ploceidae. The egg-white pattern of *Meliphaga* is unlike the ploceid pattern which resembles that of *Lichmera* because both have a visible "ovomucoid." The egg-white pattern of *Promerops* is not especially similar to that of the Ploceidae although both are Type B.

In summary, the answers to the questions posed at the beginning of this discussion seem to be as follows:

- 1) The Ploceinae and Estrildinae are related to one another more closely than either is to any other group. Although each seems to be a well-marked, readily defined group they should be placed in the same family.
- 2) The carduelines are related to the other nine-primaried oscines (fringillines, emberizines, parulines, thraupines, icterines) and are not especially close to the estrildines.
- 3) *Passer* is not as close to the estrildines and ploceines as they are to one another and not as close to the emberizines, parulines, etc. as they are to one another.

³ Payne (1969. Nest parasitism and display of chestnut sparrows in a colony of grey-capped social weavers. *Ibis*, 111: 300-307) has discovered that *Passer eminibey* builds no nests of its own but usurps the nests of *Pseudonigrita arnaudi*. Payne suggests (p. 305) that "the nest parasitism of the Chestnut Sparrow provides possible behavioural support for the ideas of relationships between the brood parasitic finches and the sparrow-weaver complex."

- 4) A family Passeridae should probably be recognized until fully convincing proof of the relationships of *Passer* is available. The relationships of *Montifringilla* are probably not with *Passer* and not with the emberizines, etc. *Montifringilla* may be closest to the Ploceidae. The status of the other genera placed by Sushkin in the Passerinae is also uncertain.
- 5) The status of the Viduinae is brought into question. They may be related to the Ploceidae but *Passer* and the emberizines must also be considered as possible close relatives.
- 6) *Bubalornis* is distinctive but is probably closest to the Ploceidae. Subfamily status in the Ploceidae is recommended. *Philetairus* is also distinctive but it may be closer to *Passer* than it is to the Ploceidae. It seems best to place *Philetairus* in the Passeridae, but to realize that the boundaries of this group are uncertain.

FAMILY VIREONIDAE, Vireos. 4/37, fig. 24.

Species examined: *Vireo gilvus*, *olivaceus*, *bellii*, *huttoni*.

Gadow (1883) placed the vireos as a subfamily in the Laniidae primarily because they have a subterminal notch on the maxillary tomium. Ridgway (1904: 233) left the Vireonidae near the shrikes although he was doubtful about a relationship between them. Pycraft (1907: 375) noted that the vireos were thought to be allied to the Sylviidae or to the Laniidae. However, in Pycraft's opinion, which was based upon osteological comparisons, only *Cyclarhis* is a laniid while *Vireolanus* is related to the Artamidae and *Vireo* to the Muscicapidae.

Most recent treatments have placed the vireos near the "New World nine-primaried oscines" at least in part because the family includes species with nine primaries and others with an extremely small tenth primary. As has been demonstrated by Averill (1925) and Hamilton (1958, 1962) there is a correlation between the development of the outer primary and the extent of migration. In those vireos which have the longest migration, the outer primary is most reduced. This produces a longer, more pointed wing, presumably an advantage for a long distance migrant.

The study by Stegmann (1962) of the rudimentary outer primary and the shape of the wing also indicates that strong flyers tend to have long pointed wings and a reduced outer primary while sedentary species, especially those living in dense vegetation, evolve rounded wings with well-developed outer primaries. These correlations render the development of the outer primary doubtful as an indicator of relationships, especially at the higher categorical levels.

Beecher (1953) interpreted his jaw muscle data to indicate that the Vireonidae are the stem group which gave rise to the other New World nine-primaried oscines. Tordoff (1954b) disputed this conclusion and suggested that the vireos (p. 281-2) "seem to have branched off from the ancestral finch stock earlier than any other living members of the New World group."

Stallcup (1954) found that certain features of the leg musculature of *Vireo* agree better with the condition in the cardinalines, emberizines, tanagers, warblers and blackbirds (icterines) than with that in the carduelines and polceids.

However, a serological study carried out by Stallcup (1961) suggested that *Vireo* is not particularly close to *Piranga* or *Cardinalis*. *Vireo*, in fact, seems set apart from most of the other oscines. Of the species tested against *Vireo* the greatest serological similarity was found with *Parus*, *Turdus* and *Passer*. *Dendroica* showed a high degree of serological correspondence with the other New World nine-primaried oscines but *Vireo* did not.

Bock (1960: 471) noted that in the opinion of many workers, including himself, the vireos are "the most likely representatives of the ancestral nine-primaried stock." Bock based this opinion upon the following points: 1) The vireos are relatively generalized insect-eaters while most of the other nine-primaried families are apparently specialized in one way or another. 2) Rejection of Tordoff's hypothesis that the free palatine process as found in the cardinals is the primitive condition eliminates one of the serious objections to the vireos being the ancestral nine-primaried oscines. 3) The vireos have a normal palatine process, a relatively unspecialized set of jaw muscles, and a tenth primary (only some species). However, Bock concludes (p. 472) by stating that "this evidence is not very conclusive and much more is needed to verify this hypothesis."

Bock (1962b) found that the Vireonidae exhibit only the beginnings of a second fossa in the head of the humerus while the New World nine-primaried oscines have the double condition.

From these several citations it is clear that there is general agreement among avian systematists today that the vireos are probably allied to the New World nine-primaried oscines, but not as closely as the members of the latter group are to one another. The egg-white data agree with this position. The Type A egg-white pattern of *Vireo* is quite simple and contains an ovalbumin region with two (or three) fractions and a conalbumin region migrating almost exactly half way between the ovalbumin and component 18. A pre-albumin is clearly present in more concentrated samples, as in the typical New World nine-primaried groups (= Fringillidae of this paper). The question that remains open is to determine just how close the vireos are to the New World nine-primaried assemblage.

The available egg-white specimens of *Cyclarhis* and *Vireolanus* are not good enough to provide a basis for discussion. Zimmer (1942) suggested that these two genera should be included in the Vireonidae. Mayr and Amadon (1951) followed Zimmer but Wetmore (1960) has retained three separate families for the vireos, peppershrikes (Cyclarhidae) and shrike-vireos (Vireolaniidae). In addition to characters cited by Pycraft (1907), Wetmore (1960: 20) notes that the dorsal pterylography of *Vireolanus* differs from that of the vireos.

THE NEW WORLD NINE-PRIMARIED OSCINES

This cumbersome and not wholly accurate phrase is sanctioned by custom to designate a large assemblage of passerine birds. They are not confined to the New World, although more numerous there in terms of species, and some passerines with nine primaries are not included. The confusion is compounded

because there is no agreement about the boundaries of the group. For example Tordoff (1954b: 273) defined the group as including "the following families of Hellmayr's *Catalogue of Birds of the Americas*: Virconidae, Vireolaniidae, Cyclarhidae, Coerebidae, Compsothlypidae (= Parulidae), Tersinidae, Thraupidae, Icteridae, Catamblyrhynchidae, and Fringillidae." This is a reasonable definition but I prefer to omit the first three families listed by Tordoff and to include the Drepanididae and the Zeledoniidae. Thus I would define the group as consisting of the families Zeledoniidae, Coerebidae, Drepanididae, Parulidae, Icteridae, Tersinidae, Thraupidae, Catamblyrhynchidae and Fringillidae of Wetmore (1960). However, I suggest that these groups be placed in a single family and that a hierarchy of subfamilies and tribes be employed. The following arrangement is proposed:

Family Fringillidae.

Subfamily Fringillinae.

Tribe Fringillini: Chaffinches, Bramblings.

Tribe Carduelini: Goldfinches, Crossbills, etc.

Tribe Drepaninini: Hawaiian honeycreepers.

Subfamily Emberizinae.

Tribe Cardinalini: Cardinals, Grosbeaks.

Tribe Emberizini: Buntings, etc.

Tribe Thraupini: Tanagers, *Tersina*.

Tribe Parulini: Wood warblers.

Tribe Zeledoniini: Wrenthrush.

Tribe Coerebini: Honeycreepers.

Subfamily Icterinae: Troupials, Blackbirds, etc.

This is not an extreme departure from current usage. This arrangement is based upon the following assumptions, the evidence for which will be presented below.

- 1) *Fringilla* is more closely related to the carduelines than to any other group.
- 2) The Hawaiian honeycreepers were derived from the cardueline finches.
- 3) The buntings, tanagers, wood warblers and honeycreepers are especially closely related to one another and the cardinals and grosbeaks are probably closest to this group.
- 4) *Zeledonia coronata* is most closely related to the wood warblers, not to the thrushes.
- 5) The troupials and their relatives are closer to the emberizines than to any other group. Perhaps they, too, should rank only as a tribe in the Emberizinae.

The inclusion of these groups in a single family recognizes their close relationships to one another and reduces the number of passerine families. The simplest way to embody these points in a classification is to utilize tribes and to depress the hierarchical structure by one or two steps. Although outside the

present area of study, this procedure should be accompanied by a correlated reduction in the number of genera to be recognized.

In my opinion this is a reasonable arrangement if it is agreed that the Estrildinae and Ploceinae are to be included within a single family, for they are probably no more closely related to one another than are any two groups within the Fringillidae as defined above.

FAMILY FRINGILLIDAE.

SUBFAMILY FRINGILLINAE.

TRIBE FRINGILLINI, Chaffinches and Bramblings. 2/3, fig. 24.

Species examined: *Fringilla coelebs*, *montifringilla*.

The determination of the relationships of *Fringilla* to other finches has produced an exceptional amount of debate. The principal questions are: 1) Is *Fringilla* most closely related to the carduelines, the emberizines or to some other group; and 2) is such a relationship close enough to warrant placing *Fringilla* within the same subfamily or family with its closest relatives or should *Fringilla* be placed in a monotypic subfamily or family?

The recent history of this debate begins with Sushkin (1925a). In this brief paper Sushkin proposed a classification as follows:

Superfamily Emberizoidei

Icteridae

Coerebidae

Tanagridae

Emberizidae

Superfamily Fringilloidei

Fringillidae (Fringillinae, Cardinalinae, Carduelinae)

Ploceidae (Passerinae, Ploceinae, Viduinae)

Drepanididae

The family Fringillidae was said by Sushkin (1925a: 37) "to consist of three distinct divisions which may be named the Cardueline, the Passerine, and the Emberizine." The Cardueline division, wrote Sushkin, "may be divided into three branches as follows: (a) includes, as far as one can judge from the genera examined, only one genus—*Fringilla*; (b), which is purely American, comprises the Cardinaline section (*Richmondia*, *Cyanocompsa*, *Oryzoborus*); while (c), mainly Palaearctic and Ethiopian, includes the rest, viz., *Carduelis*, *Carpodacus*, and *Coccothraustes*." Sushkin also stated (p. 38) that "the Cardueline division is more closely related to the Ploceo-Passerine group than to the Emberizine; and the Drepanididae seem to present another related group."

Sushkin gave no details in this rather casual paper. As the basis for his opinions he indicated only that (p. 37) "the family Fringillidae, as judged by the characters exhibited by the bony palate, the syrinx, and the external features of the horny palate, proves to consist of three distinct divisions" as noted above. Thus Sushkin seems to have been the first to suggest an especially close alliance between *Fringilla* and the carduelines. In 1925b Sushkin again presented his proposed classification with the Fringillidae consisting of the Fringil-

linae, Carduelinae and Cardinalinae. The evidence for this alliance was not presented in detail by Sushkin but several of his proposals have been accepted and incorporated into later classifications.

The key feature in Sushkin's evidence was the pattern of ridges and furrows on the palatal surface of the ramphotheca. Sushkin found that the patterns in *Fringilla* and the carduelines are alike and differ from those of the emberizines. The more extensive study by Ziswiler (1965) has confirmed Sushkin's observations.

The evidence supporting a *Fringilla*-cardueline alliance has continued to increase. Fiedler (1951) and Beecher (1953) both interpreted their jaw muscle data as indicating such a relationship and Mayr, Andrew and Hinde (1956) reviewed the anatomical evidence and added behavioral observations which they interpreted as supporting an alliance between *Fringilla* and the carduelines although they noted (p. 271) that "the behavioural evidence is certainly not conclusive." Marler (1957) pointed out that the in-flight call notes of *Fringilla* and the carduelines are similar. Andrew (1956) studied the pattern of "tail-flicks" preceding flight and found similarities between *Fringilla* and the carduelines. He suggested retaining Sushkin's arrangement, with *Fringilla* the only genus in the Fringillinae but in the same family with the carduelines. Andrew (1961) also concluded that certain movements of the males during courtship displays suggest a relationship between *Fringilla* and the carduelines.

Tordoff (1954a, b) has been one of the few to disagree with the majority viewpoint. From his study of the skull, especially the palate, he concluded that *Fringilla* is related to the emberizines while the carduelines are closer to the estrildines. Tordoff's proposed alliance between the carduelines and estrildines has been criticized and the author himself (personal communication) no longer holds this view. However, Tordoff (1954a) pointed out a number of differences between *Fringilla* and the carduelines which should not be ignored. Bock (1960: 476) however claimed that "the presence of an unfused palatine process in *Fringilla* and its apparent absence in the carduelines does not necessarily mean that the two groups are unrelated, as supposed by Tordoff."

Bock (1960: 475-477) discussed the evidence and the arguments relating to the position of *Fringilla* and concluded that (p. 476) "in several aspects of the bony palate and the jaw musculature, *Fringilla* is intermediate between the emberizine and the cardueline finches, but is closer to the carduelines." Bock (p. 476) was unable to "see any indications of a relationship between the carduelines plus *Fringilla* and the ploceids or estrildids, as advanced by Tordoff."

Ziswiler (1964) compared the feeding behavior, bill, skull, jaw muscles and their innervation and (1965) the horny palates of seed-eating birds. From these data Ziswiler concluded that *Fringilla* is related to the carduelines and, like Andrew, recommended that the Fringillinae be placed near the Carduelinae in the Fringillidae. Following a study of the gross anatomy and histology of the alimentary canal in seed-eating passerines Ziswiler (1967a) proposed that the families Fringillidae, Pyrrhuloxiidae, Ploceidae and Estrildidae be recognized as having had (p. 516) "an origin independent of" one another and "probably having arisen from different ancestors." *Fringilla* was included in the Fringillidae but Ziswiler (1967a; 516) concluded that "certain differences however advocate

setting the genus apart in a separate subfamily, Fringillinae, as opposed to the subfamily Carduelinae."

Ackermann (1967) used "numerical taxonomy" to compare a large number of measurements of the skeletal elements of *Passer*, *Fringilla* and six carduelines. He concluded that *Fringilla* exhibits relationships to the carduelines but "is clearly separable" from them at the subfamily level. He also concluded that numerical taxonomic procedures are of doubtful value in systematic ornithology. Harrison (1966) found similarities between *Fringilla* and *Carduelis* in plumage pattern and color which he interpreted as indicative of relationship between them. Mainardi (1957a, c) compared the red cell antigens of *Chloris chloris*, *Carduelis carduelis*, *C. spinus*, *C. cannabina*, and *Fringilla coelebs*. He concluded that the goldfinch is intermediate between greenfinch and chaffinch but the results are not convincing because Mainardi's "serological distances" give a value of 8 units between *C. spinus* and *C. carduelis* and 2.8 between *Chloris* and *C. carduelis* but only 1.4 between *C. carduelis* and *F. coelebs*.

Mainardi (1957b) also compared the paper electrophoretic behavior of the hemoglobins of the three species of *Carduelis* and four other carduelines with that of *Fringilla*. He discovered that *Fringilla* hemoglobin differs from that of the carduelines in having the two bands close together while in the carduelines they are more separated. Using starch gel electrophoresis Sibley et al. (in prep.) have confirmed and extended Mainardi's observations. Mainardi (1958) and Conterio and Mainardi (1959) examined additional passerine hemoglobins but the limitations of paper electrophoresis prevented them from discovering the actual range of variation among passerine groups.

A serological comparison of the red cell antigens of nine species of fringillids (Mainardi, 1958) suggested a close relationship between the Estrildinae and Passerinae on one side and between the Emberizinae and *Fringilla* on the other with the Carduelinae in an intermediate position between these two clusters. However, Mainardi noted that the hemoglobins of the carduelines and emberizines are alike and that they differ from those of *Fringilla*. Mainardi concluded that his serological data supported Tordoff (1954a) and Stallcup (1954) but not Beecher (1953).

Mainardi (1961) extended his serological comparisons to additional species of the Corvidae, Fringillidae, Ploceidae and Sturnidae. His principal conclusion was that "the Carduelines represent the bridge between *Fringilla* and the Ploceids." The difficulty here is that no comparisons were made with emberizines and other pertinent groups and Mainardi's conclusions were predicated upon the corvids being "primitive" and *Fringilla* being "more primitive than the Ploceids."

Mainardi (1960) also attempted to utilize the records of hybrids contained in Gray (1958) as data upon which to base a "degree of affinity" value among the species of fringillids, ploceids, thraupids and icterids. Mainardi concluded that *Fringilla* is closest to the carduelines, having been reported to hybridize with *Chloris*, *Pyrrhula* and *Serinus*.

Although the validity of some of the records cited by Gray (1958) has been challenged I can verify that a number of hybrids have been produced in captivity between the genus *Fringilla* and various carduelines. Specifically, in January, 1968, I obtained by purchase two adult male hybrids between a male

Greenfinch (*Carduelis chloris*) and a female Chaffinch (*Fringilla coelebs*). The plumage characters clearly show the parentage of the hybrids and the electrophoretic patterns of their hemoglobins are intermediate between those of the parental species. These and other verified records of hybrids involving *Fringilla* will be reported upon elsewhere. I have not been able to verify the reports of hybrids between *Fringilla* and *Cardinalis* or between carduelines and ploceids which were cited by Gray (1958) and used by Mainardi (1960).

It seems clear that the genus *Fringilla* is closely related to the carduelines. The remaining question is the degree of this relationship which cannot be determined from presently available evidence. However, it is instructive to note that the electrophoretic patterns of both the egg-white proteins and the hemoglobins of *Fringilla* differ from those of the carduelines and from most other fringillids.

More than 20 specimens of egg white, from both *Fringilla coelebs* and *F. montifringilla*, have been compared with over 200 specimens representing the other species of fringillids listed in the present paper. In all cases the patterns of the two species of *Fringilla* are exactly alike but they differ consistently from other fringillids, except *Cardinalis* and *Pheucticus*. These similarities and differences can be seen in the figures. The significance of these observations is unclear. The hybrids between *Fringilla* and the carduelines prove they are closely related. I have discussed the taxonomic significance of hybridization elsewhere (Sibley, 1957). The lack of hybrids between *Fringilla* and other groups proves nothing because failure to hybridize may result from genetically minor differences or, in this case, from the difficulties encountered by aviculturists in obtaining, keeping or breeding the most likely emberizines or cardinalines. For example, one reason the carduelines make good breeders in captivity is because they feed their young partly on pre-digested seeds, a simple diet to provide. Other finches require insects. Thus, although the cardueline $\times$ *Fringilla* hybrids are important as proof of close relationship it is still possible that *Fringilla* could be as close or closer to the emberizines or cardinalines. It is also true that the similarities in the egg-white protein patterns of *Fringilla* and the cardinalines could be coincidental. However, since Sushkin (1925a) also found similarities between these two groups the question warrants further study.

In conclusion, the hybrid evidence justifies the inclusion of *Fringilla* and the carduelines within the same subfamily and the cardinalines may also be related to them. This latter possibility requires additional investigation.

TRIBE CARDUELINI, Goldfinches, etc. 20/119, figs. 24, 25.

Species examined: *C. coccythraustes*; *P. pyrrhula*; *Carpodacus mexicanus*, *purpureus*, *cassinii*; *Leucosticte tephrocotis*; *C. carduelis*, *cannabina*; *C. chloris*; *Acanthis flammea*; *Spinus tristis*, *psaltria*, *lawrencei*, *barbatus*, *magellanicus*; *Serinus canaria*, *canicollis*, *sulphurata*, *mozambicus*; *Loxia curvirostra*.

The principal questions pertaining to the carduelines are: 1) Are they most closely related to the emberizines, to *Fringilla*, or to the estrildines; 2) what genera properly belong in the Carduelini; and 3) were the Hawaiian honeycreepers derived from a cardueline finch?

The first of these questions has been discussed above under the Fringillini. The existence of hybridization between *Fringilla* and the carduelines and the evidence from comparisons of the egg-white proteins and hemoglobins indicates that the carduelines are closer to the fringillines and to the emberizines than to the estrildines. The available protein data do not help to identify true cardueline genera because the electrophoretic patterns of the egg-white proteins and hemoglobins of the carduelines, emberizines, parulines and icterines are so similar. The relationships between the carduelines and the Hawaiian honeycreepers are considered below.

TRIBE DREPANININI, Hawaiian Honeycreepers. 2/22, fig. 25.

Species examined: *Psittirostra cantans*; *Loxops virens*.

Amadon (1950b) monographed this group and reviewed the history of their classification. The 22 species now recognized as members of this taxon were once scattered among several families including the finches, flowerpeckers (Dicaeidae) and honeyeaters (Meliphagidae). Later it was realized that they are actually closely related and have evolved rapidly during "recent geological periods in a favorable environment having many vacant ecological niches." (Amadon, 1947: 68). Speculation then turned to the question of the closest living relatives and several groups have been suggested as possibilities, including the Coerebini, Thraupini, Carduelini, Parulini and Icterinae.

Gadow (1891) considered only the brush-tongued oscines as possible ancestors of the Hawaiian honeycreepers and concluded that the Coerebini are their closest relatives and that the Thraupini are also related to them. Gadow also noted that the carduelines and drepaninines agreed in palatal characters. Lucas (1894) discussed several anatomical features in the Coerebini and other groups and noted that the tongue of the Hawaiian honeycreepers could have been derived from that of *Icterus* or *Dendroica*. Sushkin (1929) was impressed by the similarities in the bill, skull and horny palate between *Psittirostra* and the carduelines and proposed that the Hawaiian honeycreepers were derived from the carduelines. Amadon (1950b: 232) considered this proposal but concluded that there is a better chance that the Coerebini or Thraupini are the ancestors. Beecher (1953) found that the jaw musculature of *Psittirostra* is like that of the carduelines (*Carpodacus*) and noted (p. 312) "the striking similarity of the Hawaiian finches to the cardueline finches in all but plumage" but he dismissed the similarities as due to "parallel development from . . . thraupine stock."

Bock (1960: 477) presented a cogent argument in favor of the carduelines as the ancestors of the Hawaiian honeycreepers by pointing out that none of the anatomical characters preclude such a possibility and that the carduelines include species more capable of colonizing the Hawaiian Islands than any of the other groups that have been suggested.

The egg-white protein data lend support to the theory that the carduelines provided the hardy overseas immigrant ancestor of the Hawaiian honeycreepers. The evidence is rather subtle because all of the New World Fringillidae have similar egg-white patterns. However, in both the starch gel and disc gel pat-

terns of *Loxops*, *Psittirostra* and the carduelines there is a tendency for the conalbumins to migrate more slowly than in the emberizines, etc. This produces a pattern with (usually) relatively more space between the conalbumin and ovalbumin regions. The difficulty is that this condition is neither constant nor large enough to be easily demonstrated. This will seem to be a flimsy basis for supporting the cardueline theory of drepaninine ancestry but, coupled with the other evidence, it seems the most probable. One can even point to the crossbills, *Loxia*, as possibly closest to what the ancestor must have been. They are strong-flying nomads which travel in flocks and, perhaps most importantly, can breed at any time of year if the food supply is favorable. As noted by Bock (1960) these properties, plus the lack of important obstacles to the theory, make some cardueline, possibly *Loxia*, the most probable ancestor of the Drepaninini. Perhaps it is more than convergence that the mandibles of *Loxops coccinea* are slightly crossed. Perkins (quoted by Amadon, 1950b: 201) noted that *L. coccinea* uses its bill to open leaf-buds much as *Loxia* opens pine cones.

Thus, although final proof is not yet available, the weight of evidence favors the carduelines as the closest living relatives of the Drepaninini.

SUBFAMILY EMBERIZINAE.

TRIBE CARDINALINI, Cardinals, grosbeaks, etc. 8/132, fig. 25.

Species examined: *Cardinalis cardinalis*; *Pheucticus ludovicianus*; *Paroaria capitata*; *Passerina cyanea*, *versicolor*; *Cyanocompsa cyanea*, *cyanoides*; *Spiza americana*.

TRIBE EMBERIZINI, Buntings, etc. 54/171, figs. 25, 26, 27.

Species examined: *Arremonops conirostris*, *rufivirgatus*; *Arremon flavirostris*; *Pipilo erythrophthalmus*, *ocai*, *fuscus*, *albicollis*, *rutilus*; *Melospiza kieneri*; *Atlapetes semirufus*; *Calamospiza melanocorys*; *Passerculus sandwichensis*; *Ammodramus savannarum*; *Ammospiza maritima*; *Chondestes grammacus*; *Spizella passerina*, *arborea*; *Junco phaeonotus*; *Zonotrichia capensis*, *querula*; *Passerella iliaca*; *Melospiza georgiana*, *lincolni*, *melodia*; *Calcarius ornatus*, *pictus*, *lapponicus*; *Plectrophenax nivalis*; *Emberiza schoeniclus*, *citrinella*, *melanocephala*, *flaviventris*, *calandra*, *cia*, *cirlus*, *caesia*; *Geospiza fortis*, *fuliginosa*, *magnirostris*; *Poospiza melanoleuca*, *nigrorufa*; *Embernagra platensis*; *Loxigilla violacea*; *Diuca diuca*; *Sporophila aurita*, *nigricollis*; *Sicalis flaveola*, *luteola*; *Phrygilus fruticeti*; *Coryphospingus cucullatus*; *Saltator atriceps*, *maximus*, *aurantiiostris*, *coerulescens*.

TRIBE THRAUPINI, Tanagers. 19/196, figs. 27, 28.

Species examined: *Thraupis cyanoptera*, *palmarum*, *virens*, *sayaca*, *ornata*, *abbas*, *bonariensis*, *episcopus*; *Tanagra aurea*, *chlorotica*; *Tangara cyanoventris*, *icterocephala*; *Habia gutturalis*, *rubica*; *Tachyphonus rufus*, *coronatus*; *Piranga olivacea*; *Rhodinocichla rosea*; *Tersina viridis*.

TRIBE PARULINI, Wood warblers. 17/109, fig. 28.

Species examined: *Mniotilta varia*; *Vermivora ruficapilla*, *celata*; *Peucedramus taeniatus*; *Dendroica petechia*, *caerulescens*, *pennsylvanica*, *striata*, *discolor*; *Oporornis tolmiei*; *Geothlypis trichas*; *Chamaethlypis poliocephala*; *Icteria virens*;

Cardellina rubrifrons; *Setophaga ruticilla*; *Myioborus miniatus*; *Basileuterus rufifrons*.

TRIBE ZELEDONIINI, Wrenthrush. 1/1, fig. 28.

Species examined: *Zeledonia coronata*.

TRIBE COEREBINI, Honeycreepers. 1/36, fig. 28.

Species examined: *Coereba flaveola*.

SUBFAMILY ICTERINAE, Troupials, blackbirds, etc. 32/88, figs. 28, 29.

Species examined: *Dolichonyx oryzivorus*; *Sturnella magna*, *neglecta*; *X. xanthocephalus*; *Agelaius phoeniceus*; *tricolor*, *ruficapillus*, *thilius*, *icterocephalus*; *Icterus galbula*, *chryscephalus*, *gularis*, *pustulatus*, *chrysater*; *Euphagus cyanocephalus*; *Cassidix mexicanus*, *nicaraguensis*; *Quiscalus quiscula*, *lugubris*; *Molothrus ater*, *badius*, *bonariensis*, *rufoaxillaris*; *Tangavius aeneus*; *Scaphidura oryzivora*; *Pezites militaris*; *Pseudoleistes virescens*; *Dives dives*; *Psarocolius angustifrons*; *Cassiculus melanicterus*; *Zarhynchus wagleri*; *Cacicus cela*.

These groups are considered together because an impressive array of evidence indicates that they are closely related. Except for characters associated with diet the members of the Emberizinae and Icterinae are remarkably uniform. The postcranial skeleton shows little or no variation associated with subgroups (Tordoff, 1954a; Bock, 1962b); the jaw musculature shows variation presumably associated with diet but a basic plan is shared by all members (Beecher, 1953); the tissue proteins indicate close relationship (Stallcup, 1961) and certain behavior patterns are common to all members (Andrew, 1956). In spite of some differences between the Icterinae and Emberizinae in behavior (Andrew, 1961) there is a clear consensus that the buntings, cardinals, tanagers, honeycreepers, wood warblers and troupials are closely related.

The electrophoretic patterns of the egg-white proteins and hemoglobins support this view. Except for minor variations in the mobilities of some components all available species of these groups, with the possible exception of some Cardinalini, have electrophoretically identical egg-white proteins and hemoglobins. Since it is not possible to recognize subgroups from the presently available protein evidence the arrangement presented here is based upon other classifications. The data indicate the close relationships among all of these groups and the suggested arrangement seeks to express this fact by reducing the number of families.

The Icterinae seem to be fairly well separated from the Emberizinae although *Spiza* has been placed in the Emberizinae by Tordoff (1954a) and in the Icterinae by Beecher (1953).

The emberizines merge with the cardinals and tanagers and the tanagers merge with the warblers. On the basis of the jaw musculature and characters of the horny palate Beecher (1951) proposed that the Coerebidae (Wetmore, 1960) is a composite of nectar-feeding warblers and tanagers. Beecher proposed that a tribe Coerebini should be recognized in the Parulidae to contain the genera *Coereba*, *Atelodacnis* and *Conirostrum*. De Schauensee (1966: 454) has challenged this procedure and Moynihan (1968) has discussed the ecology and behavior of these genera. The tribe Coerebini in the present paper is

employed merely to indicate that the New World honeycreepers are allied to the tanagers and wood warblers. The egg-white patterns would not be expected to be useful in distinguishing thraupine honeycreepers from paruline honeycreepers because the two groups themselves cannot be separated. *Tersina* and *Catamblyrhynchus*, sometimes placed in monotypic families, subfamilies or tribes, are of uncertain rank. If the entire set of categories is to be moved up or down such genera can be elevated or depressed according to the taste of the reviewer. In my opinion the overwhelming fact to be expressed at the level of subfamilies is the remarkable compactness of this entire group, not the special adaptations of certain species.

Zeledonia coronata was long thought to be a thrush or to be closely related to the thrushes. Its actual affinities seem to be with the wood warblers and to indicate this relationship I have placed it adjacent to the Parulini but in a separate tribe, Zeledoniini, in recognition of its specialized characters and to call attention to its new location in the classification. I have reviewed the taxonomic history of *Zeledonia* (Sibley, 1968) and the evidence linking it with the wood warblers, rather than with the thrushes. The vernacular name "wrenthrush" seems to be an appropriate modification of "wren-thrush," following the precedent of waterthrush, etc.

These several subfamilies and tribes probably represent clusters of species having similar feeding adaptations; the Emberizini are mostly seed-eating ground feeders, the Cardinalini mostly eat larger, harder seeds, the Thraupini feed largely on fruits, the Parulini on insects and the Coerebini on nectar. The Icterinae eat a variety of foods and most of them have a similar straight bill which, like the starlings, they use to open fruits, to probe crevices, etc. by inserting the closed bill and then opening it (Lorenz, 1949). Bowman (1961: 31) observed that *Geospiza scandens* uses this same method when feeding on green bananas.

It is thus entirely possible that these taxonomic subdivisions actually delimit major feeding niches, not the genetically most natural groups. The adaptive radiation so easily observed in the Galapagos finches (Lack, 1945; Bowman, 1961) and in the Hawaiian honeycreepers (Amadon, 1950; Baldwin, 1953b) must also have occurred on the continents. It is therefore highly probable that some "warblers" are more closely related to some "tanagers" than they are to other "warblers," and so on. The Galapagos finches provide a synopsis of the more complex continental situation and Bowman (1961) has provided the evidence from his detailed study of the correlations between variations in morphology and diet. Bowman found that essentially all of the structural differences in bill, digestive tract, jaw muscles, skull, horny palate, tongue and hyoid bones were related to differences in food habits. For example, the finch-billed *Geospiza magnirostris* takes 80% seeds and 10% insects while *G. scandens* with a more slender bill and deeply cleft tongue takes 20% of its food as nectar and the remainder as small seeds and insects. The warbler-finch, *Certhidea olivacea*, which feeds entirely upon insects, has the most slender bill of all and was for a long time placed with the paruline warblers.

Similar correlations are described by Bowman for the other anatomical features listed above. With reference to the horny palate Bowman (1961: 162)

notes that "In view of the great variation in the palatal relief of twelve species of the Geospizinae, I am impelled to reemphasize the remark by Lowe (*in* Sushkin, 1925a: 39): 'in any classification the use of characters based on the modification due to feeding habits [is] not as reliable as the employment of anatomical characters, not so prone to be affected.' " Bowman further states (p. 162) that "so far as the Geospizinae as a group are concerned, the horny palate does not show 'great conservatism' (cf. Beecher, 1953: 275)." The differences observed by Bowman (p. 295) in the configuration of the horny palate "are functionally related to differences in diet." These functional correlations demonstrated by Bowman must be considered when evaluating the taxonomic conclusions which Ziswiler (1964, 1965, 1967a, b) has proposed. Nectar-feeding niches were more numerous in the Hawaiian Islands and thus the presumed cardueline ancestor radiated rapidly to fill them. In both archipelagos the opportunities for dispersal, divergence, and re-invasion made speciation possible.

On the continents the same forces are at work but the tidy picture becomes obscured because so many more species are involved, intermediate niches are present, barriers are less precise and a greater time span is involved. Being unable to sort out the genetically related groups using gross morphology we compromise by setting up groups based upon the feeding structures because they are the only characters which show significant variation. The reason we can see what appear to be groups is because the major feeding niches are fairly discrete, not a smooth continuum. Where there are intermediate feeding niches we encounter intermediate species and the boundaries of taxa based upon the feeding structures become blurred.

Natural groups larger than genera must exist on the continents, as they do in the Galapagos and Hawaiian archipelagos, but we should not expect to be able to delineate them by characters of the bill, the palate, the jaw muscles, the digestive tract or any other structure intimately concerned with feeding. A classification based upon such evidence cannot avoid being, in part, a classification of food niches.

DISCUSSION AND SUMMARY

Ten years ago Stresemann (1959) recorded his doubts about the ability of "comparative morphology, comparative physiology [and] comparative ethology" to provide trustworthy evidence of the relationships of the higher categories of birds. I agreed with Stresemann's argument but declined to accept his conclusion that the situation was hopeless because new techniques, including the comparative study of protein structure, were "just beginning to be utilized" (Sibley, 1960: 215-216). Although progress has been slow and spectacular results have not been achieved I continue to be optimistic. This optimism is based upon three facts. First, the theoretical basis for the belief that protein molecules contain large amounts of evolutionary information has been repeatedly confirmed and strengthened during the past decade. Second, the number of systematists utilizing "molecular" or "biochemical" techniques has steadily increased and third, the techniques themselves have undergone constant improvement. Much of this improvement has been accomplished through the development of better instruments and, at the present time, we are witnessing the most promising development in many years, namely, an automatic instrument which will determine the amino acid sequences of protein molecules. This "sequenator" (Edman and Begg, 1967), of which several examples have been constructed, is expected to be commercially available within a short time. The existence of such instruments is ample justification for continuing optimism.

Although there is a certain consolation in faith in the future it is more to the point to evaluate the accomplishments of the past and specifically of the work reported in the present paper. Some will be disappointed in the lack of "conclusions" or "proved" results. However, systematics consists of statements of opinions derived from evaluations of various kinds of evidence and such evaluations are, at best, probability estimates as Throckmorton (1968) has stated. The evidence available to us up to this time has permitted relatively few "highly probable" judgments to be rendered. Therefore the principle contribution of this study has been to identify a number of situations which can be evaluated as "probable" or "possible." The formulation of these questions, some of which are novel while others are traditional, is, in my opinion, the principle contribution of this study. These questions are presented in a following section. The next step should be to seek additional evidence which will improve the probability estimate of each question.

Some of the questions referred to above and defined in a following section pertain to the degrees of genetic relatedness among the presently recognized families of passerine birds. The nature of this general problem is exemplified by the Fringillidae and has been discussed on pages 106-108.

The closely related subgroups of the Fringillidae include the seed-eating fringillines, carduelines, emberizines and cardinalines but each of these in turn has evolved differences in feeding apparatus and behavior. Competition among

related sympatric species is presumably one source of selection which produces such differences. The fruit-eating thraupines, insect-eating parulines, nectar-feeding coerebines and drepaninines, and the relatively omnivorous icterines also belong to the fringillid assemblage. If other such natural assemblages exist, they, too, may be expected to be composed of subgroups, each adapted to feed upon somewhat different foods. Beecher (1953) saw this problem clearly, but his attempts to solve it may have been frustrated because his own data, derived from comparisons of the jaw muscles, were themselves, in some cases at least, reflecting convergence due to similar food habits. On the other hand some of the assemblages recognized by Mayr and Amadon (1951) may be convergently similar clusters based largely upon feeding habits. The "Primitive Insect Eaters," the "Shrikes and Allies" and the "Old World Nectar Eaters" are possible examples. However, Mayr and Amadon (1951) also recognize an assemblage of "Vireos, Finches and Allies" (= Vireonidae and Fringillidae of this paper) which is probably a natural unit composed of subgroups with diverse feeding habits and feeding structures, as noted above.

Although the Galapagos finches, the Hawaiian honeycreepers and the entire assemblage of Fringillidae have been unmasked as clusters of closely related species there is no reason to expect that the members of similar, but as yet unrecognized assemblages will readily be identified. For one thing, the fringillids must have evolved recently, for they are alike in so many characters. Some of the undiscovered groups will have diverged much earlier and will thus have had more time to accumulate differences as well as to refine their convergent similarities to unrelated groups. The task will not be easy but until the hypothesis itself is discredited it should be attempted.

I propose to make such an attempt but I want to make it clear that I do not consider the electrophoretic pattern data to be free of pitfalls. There is no reason to expect these data to reflect food habits but they are vulnerable to similarities due to *electrophoretic coincidence* which has been discussed on page 17. Electrophoretic coincidence is likely to be an important hazard only when comparing single proteins of uncertain homology. It is less likely to be important when comparisons are made between complex systems of homologous proteins such as avian egg white. However, because the possibility of coincidental similarities in patterns does exist, I feel obliged to emphasize that the assemblages I will designate are presented as possibilities to be tested, not as conclusions to be defended.

As the egg-white protein data have accumulated over the past several years, it has become apparent that closely related species have extremely similar or identical electrophoretic patterns. Many examples have been noted in the family accounts in this paper and can be confirmed by reference to the illustrations. Especially convincing examples include the Corvidae, Ploceidae and Fringillidae, as defined herein. The evidence from such large groups of species provides the strongest support for the belief that the species composing natural assemblages do have similar egg-white protein electrophoretic patterns.

It has also become clear that there are relatively few basically different patterns in the passerines and that, in some cases, families sharing the same pattern have not been considered to be related. The question is obvious. If

groups known to be closely related share similar patterns, what should we conclude about groups sharing similar patterns but not suspected of being closely related? Clearly there are two possibilities; 1) that the similarities are due to coincidence, which is a possibility as I have repeatedly emphasized, or 2) that the similar patterns may be directing our attention to assemblages of related species.

Because of the limited ability of electrophoresis to provide an index to the genetic information content of protein molecules the possibility of coincidental similarities must be tested by additional techniques, such as those used by Sibley (1964), Corbin (1968) and Sibley, Corbin and Haavie (1969).

Until such tests can be applied to this question it will remain merely an intriguing hypothesis but, to permit others to examine it in relation to evidence from other sources, I will define some of the hypothetical assemblages that the protein data seem to suggest. In so doing I am merely pointing out the distribution of grossly similar egg-white protein electrophoretic patterns. I am neither stating nor implying that these similarities prove that the large assemblages so defined are composed of the most closely related groups. However, within the large units, which have been designated as "Pattern Types," (p. 20) I will define a series of "Groups" and will indicate the degree of confidence I attach to the probability that the members of such groups are related to one another. This analysis will also function as a summary of the comparisons and suggestions presented under the family accounts.

It will be apparent, as noted under the family accounts, that the egg-white protein data do not support some of the alliances that have been proposed in the past. In most cases, however, they do not oppose the present classification except to suggest that larger assemblages than have been recognized may exist.

"PATTERN TYPE A"

GROUP 1. Sylviidae, Muscicapidae, *Prunella*. These three groups probably form a natural unit. *Aegithalos* and *Psaltiriparus*, which are probably congeneric, may also be quite close to the sylviids. Others that may belong in Group 1 are *Chamaea*, *Zosterops*, the Mimidae, and the Motacillidae. The exceptional situation in *Prinia* has been discussed under the Turdidae (p. 71). *Acanthiza* and *Sericornis* have Type B patterns and are discussed below under Type B, Group 8.

GROUP 2. The Meliphagidae present a special problem which has been discussed under the family account. The genera *Meliphaga*, *Phylidonyris* and *Xanthomyza* have Type A patterns. *Lichmera*, *Certhionyx* (and possibly *Meliornis*) are Type B. This situation may be similar to that in *Prinia*, i.e., the difference may be due to a change in the mobility of one fraction. Thus the difference may be either genetically important or unimportant. It will require additional studies to determine the significance of these observations.

GROUP 3. *Parus* and *Certhia* are probably related to one another and they may be closest to Group 1. Furthermore, although the Troglodytidae have a

distinctive pattern it has some aspects in common with those of *Parus* and *Certhia*. The *Parus-Certhia* pattern also resembles those of some fringillids, especially the carduelines.

GROUP 4. Fringillidae, including the fringillines, carduelines, drepaninines, emberizines, cardinalines, thraupines, coerebines, parulines, *Zeledonia* and icterines; Vireonidae. The fringillids are certainly closely related to one another and the vireos are probably close to them.

GROUP 5. *Passer* and *Vidua*. These two have similar egg-white patterns and may be related more closely to one another and to the Fringillidae than to the Ploceidae.

GROUP 6. Alaudidae. The larks have a Type A pattern which, as noted in the family account, is much like that of the emberizines, sylvids and motacillids. This does not prove that the larks are related to these groups but they could be.

GROUP 7. Hirundinidae. The swallows seem to have a Type A pattern but in some there is a tendency for the post-albumin area to resemble an "ovomucoid" component. Their relationships remain obscure.

GROUP 8. Timaliidae. The babblers have a pattern that fits the definition of Type A but they have a stronger cathodal fraction than is usually present in passerines and there may be an "ovomucoid" component. The relationships of the babblers thus remain uncertain.

GROUP 9. Grallinidae. *Grallina* apparently has a Type A pattern but the available material is poor and conclusions cannot be drawn.

GROUP 10. Pittidae. The pittas seem to lack a separate "ovomucoid" and thus fall in Type A but no taxonomic conclusions can be drawn from this.

"PATTERN TYPE B"

GROUP 1. Turdidae. Most thrushes have a typical Type B pattern but in *Sialia*, *Erythropygia*, *Copsychus* and *Cossypha* there seems to be but one fast fraction in the more concentrated samples. In dilute specimens it can be seen that there are separate "ovomucoid" and ovalbumin regions but that they are very close together, hence they merge in concentrated specimens.

GROUP 2. Pycnonotidae and Dicruridae. These two families may be related to one another but the evidence is not yet completely convincing. The egg-white pattern of *Sturnus* resembles those of *Pycnonotus* and *Dicrurus* but the "ovomucoid" and ovalbumin regions in *Sturnus* are slower.

GROUP 3. Oriolidae. The pattern of *Oriolus* shows both a visible "ovomucoid" and strong pre-albumins in concentrated samples. It differs from the patterns of *Pycnonotus* and *Dicrurus* in the mobilities of the fractions in the ovalbumin region and in the strong pre-albumin. *Oriolus* is of uncertain relationships and is left in a separate group pending the development of better evidence.

GROUP 4. Nectariniidae. The sunbirds have an "ovomucoid" component and thus are Type B but their closest relatives remain obscure. I doubt that they are closely related to the Meliphagidae.

GROUP 5. Ploceidae. The ploceines and estrildines have a strong "ovomucoid," thus differing from *Passer* and *Vidua* which lack it and are thus Type A. The significance of such a difference is not yet clear but it is impressive that the 30 available species of ploceines, 29 estrildines, four viduines and five *Passer* are consistent in their respective patterns.

GROUP 6. Sturnidae. In *Sturnus*, *Spreo*, *Acridotheres* and *Sturnia* the pattern is Type B with a separate "ovomucoid." In *Lamprotornis* and *Onychognathus* the "ovomucoid" merges with the ovalbumin region in concentrated samples. This situation seems to be similar to that in the thrushes. Several groups have patterns similar to that of *Sturnus* including *Promerops*, *Artamus*, *Pycnonotus* and *Dicrurus*.

GROUP 7. Cracticidae and Paradiseidae. These two families seem to have an "ovomucoid" fraction and are alike in the ovalbumin region. They may differ in the conalbumin region but better material will be needed to resolve this question. They seem more like one another than either one is like the Corvidae, hence a relationship between them seems probable. However, *Diphyllodes* also shows some resemblance to the Meliphagidae in the ovalbumin region.

GROUP 8. *Lichmera*, *Certhionyx*, *Pardalotus*, *Acanthiza*, *Sericornis*. These five genera have visible "ovomucoid" fractions and all are Australian. *Lichmera* and *Certhionyx* are usually placed in the Meliphagidae, *Pardalotus* in the Dicaeidae and *Acanthiza* and *Sericornis* in the Sylviidae. *Lichmera* and *Certhionyx* have essentially identical patterns. The others are similar to them and to one another but differences are also easily seen. This situation raises the possibility that these Australian genera might be related to one another more closely than to the typical meliphagids, dicaeids and sylvids with which they are currently placed. This is only a highly tentative hypothesis to be tested by other techniques.

GROUP 9. Non-oscines. The non-oscines, except *Pitta*, seem to have an "ovomucoid" fraction, hence are Type B. Some formicariid patterns appear to lack the "ovomucoid" but dilute samples show that it is merely close to the ovalbumin and appears to merge with it in concentrated specimens.

Within the non-oscines it is possible to see that the patterns of the members of each family resemble one another closely and that the New World groups are more similar to one another than any one of them is to any Old World group.

Whether or not some of the non-oscines are actually more closely related to oscines than to other non-oscines still remains an open question.

Other genera which have Type B patterns, but which do not fit well into any of the above groups, include *Sitta*, *Climacteris* and *Panurus*. *Tichodroma* may have an "ovomucoid" but it is not typical. The relationships of these genera are uncertain.

Phainopepla, *Bombycilla* and *Dulus* also have Type B patterns but only *Bombycilla* is based on excellent samples. The patterns of *Phainopepla* and *Bombycilla* are similar to one another and they may be related but *Dulus* has a distinctly different pattern and may not be close to *Bombycilla* and *Phainopepla*.

"PATTERN TYPE C"

The Corvidae, *Lanius* and *Campephaga* have Type C patterns. Since other evidence suggests that the corvids and *Lanius* are related it seems probable that they are. Whether or not *Campephaga* is also related to the Corvidae is uncertain.

The patterns of *Chlorophoneus*, *Urolestes*, *Telophorus* and *Nilaus* also fall in Type C. That of *Laniarius* differs and probably should be considered Type B.

"PATTERN TYPE D"

This pattern occurs in the wrens (Troglodytidae) thus seeming to set them apart from other oscines. However, some aspects of the Type D pattern are also found in those of *Parus* and *Certhia* which have Type A patterns. The wren pattern also shows some similarities to those of the non-oscines, for example the Furnariidae and Tyrannidae, but these similarities may only be coincidental. The situation is impossible to evaluate and must be tested using other techniques.

Whether or not the major pattern types indicate large assemblages of related groups or merely coincidentally similar electrophoretic patterns will have to be tested. However the families and genera in some of the "groups" do seem to be closely related and some of these combinations represent departures from traditional classifications. I do not propose to defend the suggestions in this paper but rather to seek additional data to test them. These new data will come partly from additional studies of the egg-white proteins, from comparative studies of other proteins, for example hemoglobins, from comparisons of the tryptic peptides of certain single proteins, possibly ovalbumin and hemoglobin and from immunological data. These procedures will, in many cases, still fall short of providing satisfactory proof but they are steps in the direction of the ultimate goal of comparative studies of protein structure, namely, amino acid sequences.

PROBABILITIES AND POSSIBILITIES

All taxonomic opinions are probability estimates and, according to Throckmorton (1968: 387), "phylogenetic taxonomy cannot produce absolute answers, . . ." The electrophoretic data presented in this paper are new but like all previous data they too are incapable of producing absolute answers. Therefore, instead of "conclusions," which imply a high degree of certainty, the following section presents a series of statements under the headings "Highly Probable," "Probable," "Possible" and "Improbable." These statements are synopses of the dis-

cussions in the text and in the preceding section which defined "groups" of pattern types. The statements are subjective judgments based upon the evidence known to me, strongly influenced by the electrophoretic patterns but not solely dependent upon them. The statements pertain to previously proposed alliances, to the new data presented in this paper, or to both.

HIGHLY PROBABLE

The following statements should be prefaced with "It is highly probable that . . ."

- 1) the New World non-oscine passerine groups are more closely related to one another than any one of them is to any Old World group.
- 2) *Aegithalos* and *Psaltiriparus* are closely related to one another.
- 3) the Ploceinae and Estrildinae are more closely related to one another than either is to any other group.
- 4) the carduelines are related to the other Fringillidae and are not especially close to the Estrildinae.
- 5) *Zeledonia* is most closely related to the wood warblers, not to the thrushes.

PROBABLE

"It is probable that . . ."

- 1) the cotingas, manakins (Pipridae) and plant-cutters (*Phytotoma*) are more closely related to one another than any one of them is to some other group.
- 2) the New Zealand wrens (Acanthisittidae) and the pittas (Pittidae) are each more closely related to some group of Old World oscines than to the New World non-oscines.
- 3) the Corvidae are more closely related to the Laniidae than to any other group.
- 4) the Cracticidae and Paradiseidae are more closely related to one another than either is to the Corvidae.
- 5) *Cinclus* is related to the Turdidae.
- 6) the Sylviidae, Muscicapidae and *Prunella* are more closely related to one another than any one of them is to the Turdidae.
- 7) *Bombycilla* and *Phainopepla* are more closely related to one another than either is to *Dulus*.
- 8) the vireos are more closely related to the New World nine-primaried oscines than to any other group.
- 9) *Fringilla* is more closely related to the carduelines than to any other group.
- 10) the Drepaninini were derived from the Carduelini.

POSSIBLE

The following statements could also be phrased as questions. They represent the 50% level of certainty and present the most interesting group of problems for further investigation.

"It is possible that . . ."

- 1) the Philepittidae and Eurylaimidae are closely related.
- 2) some genera of dendrocolaptids should be transferred to the Furnariidae, and vice versa (*vide* Feduccia, personal communication).
- 3) the Campephagidae are more closely related to the Corvidae than to any other group.
- 4) *Parus* and *Certhia* are closely related.
- 5) *Parus* and *Certhia* are more closely related to *Sylvia*, *Muscicapa* etc. than to any other groups.
- 6) *Chamaea* is a sylviid.
- 7) *Aegithalos* and *Psaltiriparus* are sylviids.
- 8) the bulbuls are most closely related to the drongos, the starlings and/or the Old World orioles.
- 9) *Acanthiza* and perhaps *Sericornis* are closer to certain meliphagids (*Lichmera*, *Certhionyx*) than to the sylviids.
- 10) *Epthianura* is closer to *Meliphaga* than to *Sylvia*.
- 11) *Rhipidura* is not a muscicapid.
- 12) *Sphenostoma* is not a muscicapid.
- 13) *Rhipidura* and *Sphenostoma* are closely related.
- 14) the Motacillidae are most closely related to the Sylviidae and Muscicapidae.
- 15) *Artamus*, *Pycnonotus* and *Dicrurus* are related to *Sturnus*.
- 16) *Promerops* was derived from the starlings.
- 17) *Nilaus* is a laniid.
- 18) the Meliphagidae are composed of two subgroups.
- 19) *Pardalotus* and *Dicaeum* are not closely related.
- 20) *Pardalotus* is more closely related to certain honeyeaters than to *Dicaeum*.
- 21) *Zosterops* is more closely related to the sylviid-muscicapid assemblage than to the nectariniids or dicaeids.
- 22) *Passer* is not a ploceid.
- 23) *Vidua* is closely related to *Passer*.
- 24) *Vidua* is not as closely related to the ploceines and estrildines (Ploceidae) as it is to *Passer*.
- 25) *Passer* and *Vidua* are more closely related to the Fringillidae than to the Ploceidae.
- 26) *Fringilla* is as closely or more closely related to the cardinaline finches than to the cardueline finches.

IMPROBABLE

"It is improbable that . . ."

- 1) the broadbills are closely related to the pittas.
- 2) the larks are closely related to the Ploceidae.
- 3) the Corvidae are closely related to the Paridae.
- 4) *Panurus* is a timaliid or that *Panurus* is a parid.

- 5) *Cinclus* is closely related to the Troglodytidae.
- 6) the Mimidae and Troglodytidae are closely related.
- 7) the Troglodytidae and Turdidae are closely related.
- 8) the Motacillidae are closely related to *Panurus*.
- 9) *Nilaus* is a muscicapid.
- 10) *Zosterops* is closely related to the dicaeids or nectariniids.

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FIGURES 3 to 38

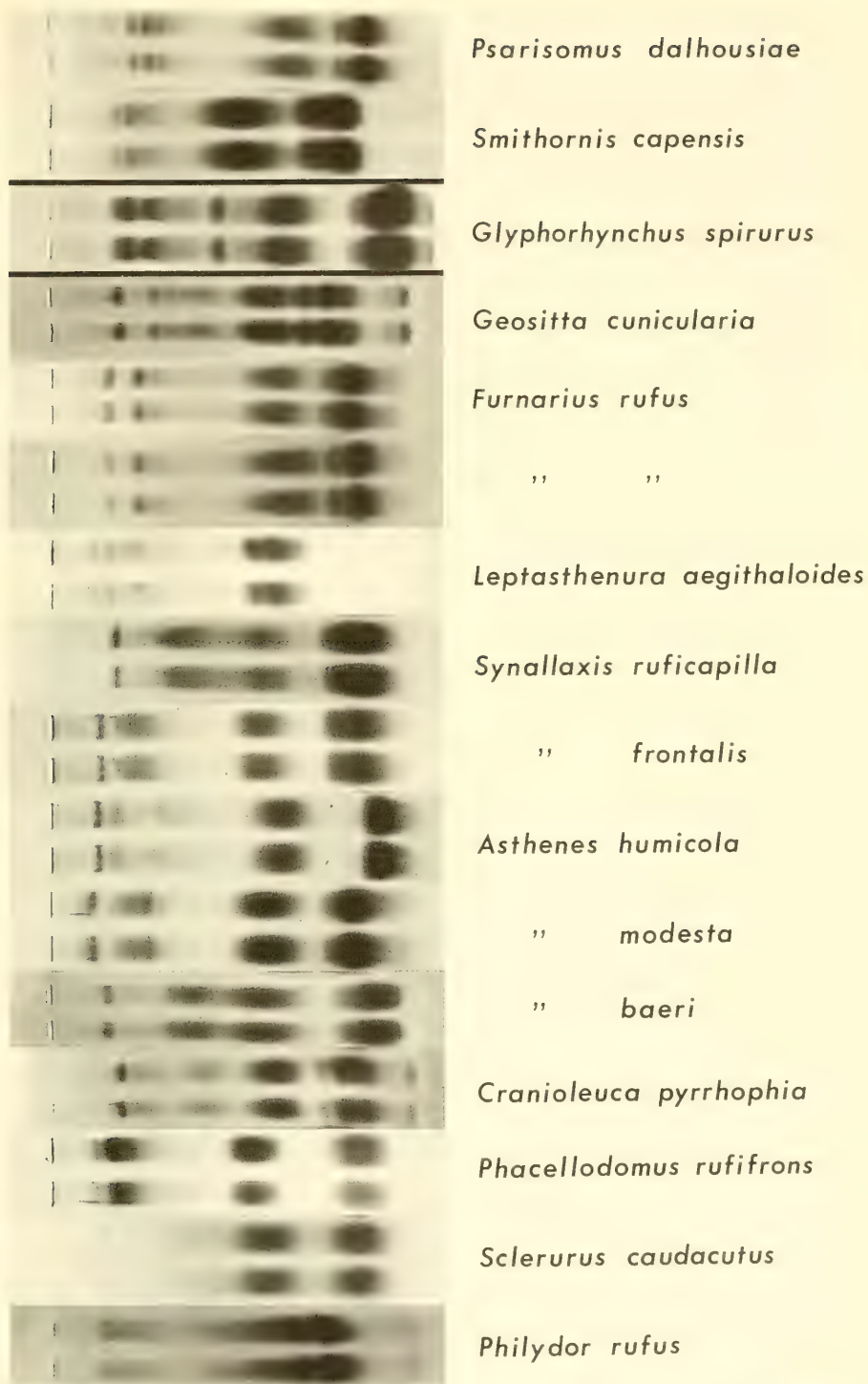


FIGURE 3. Starch gel electrophoretic patterns of the Eurylaimidae, Dendrocolaptidae, and Furnariidae.

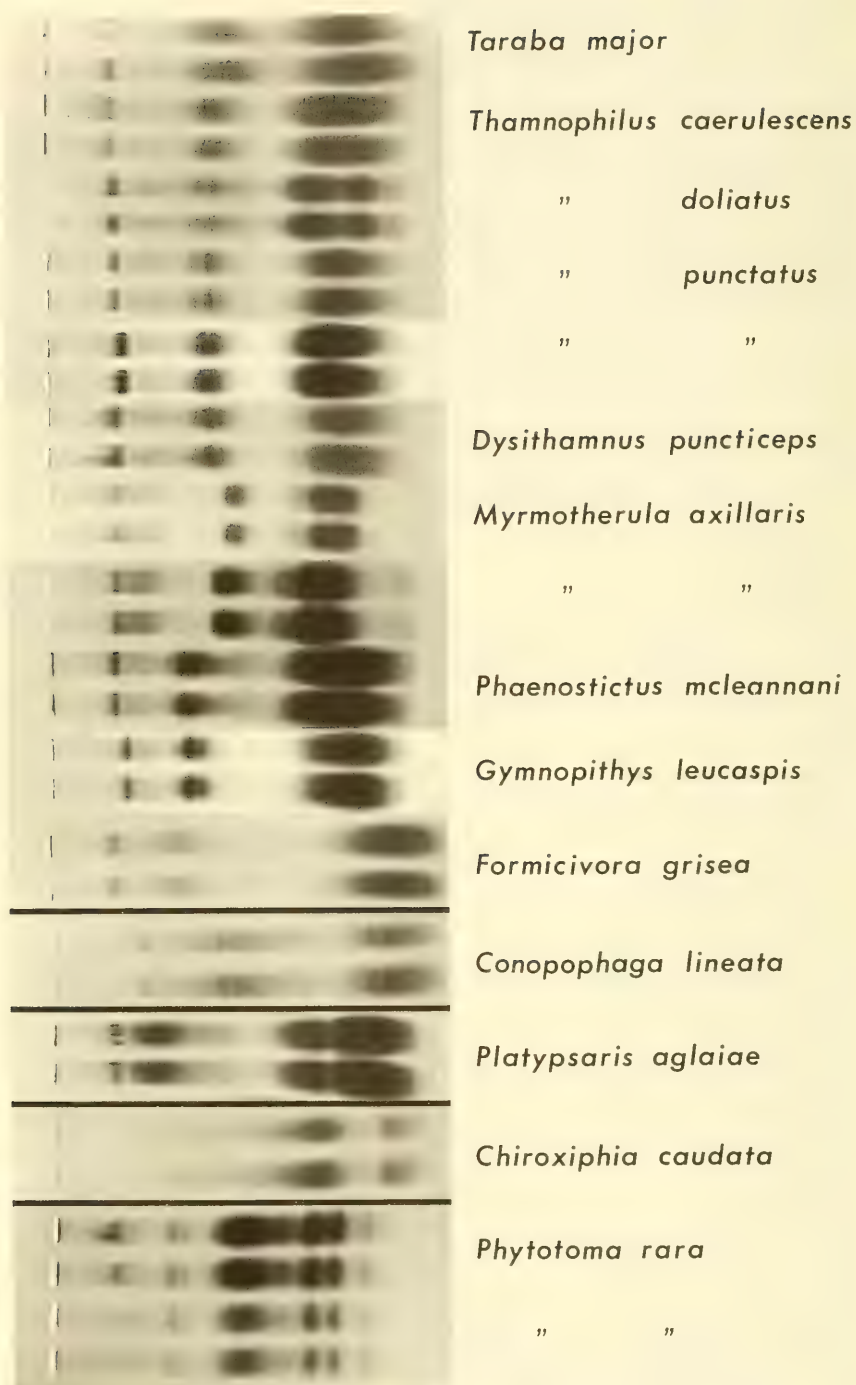


FIGURE 4. Starch gel electrophoretic patterns of the Formicariidae, Conopophagidae, Cotingidae, Pipridae and Phytotomidae.

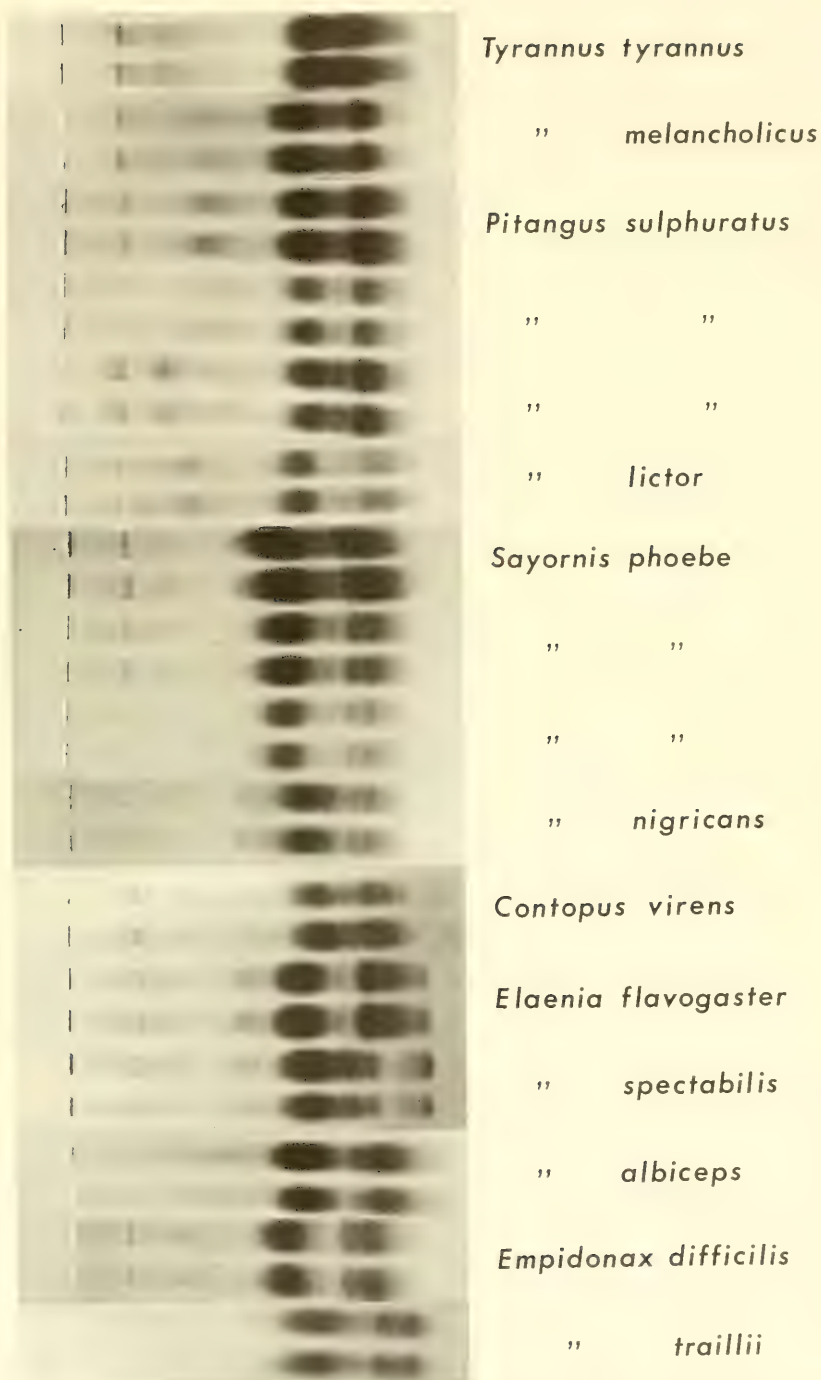


FIGURE 5. Starch gel electrophoretic patterns of the Tyrannidae (part).

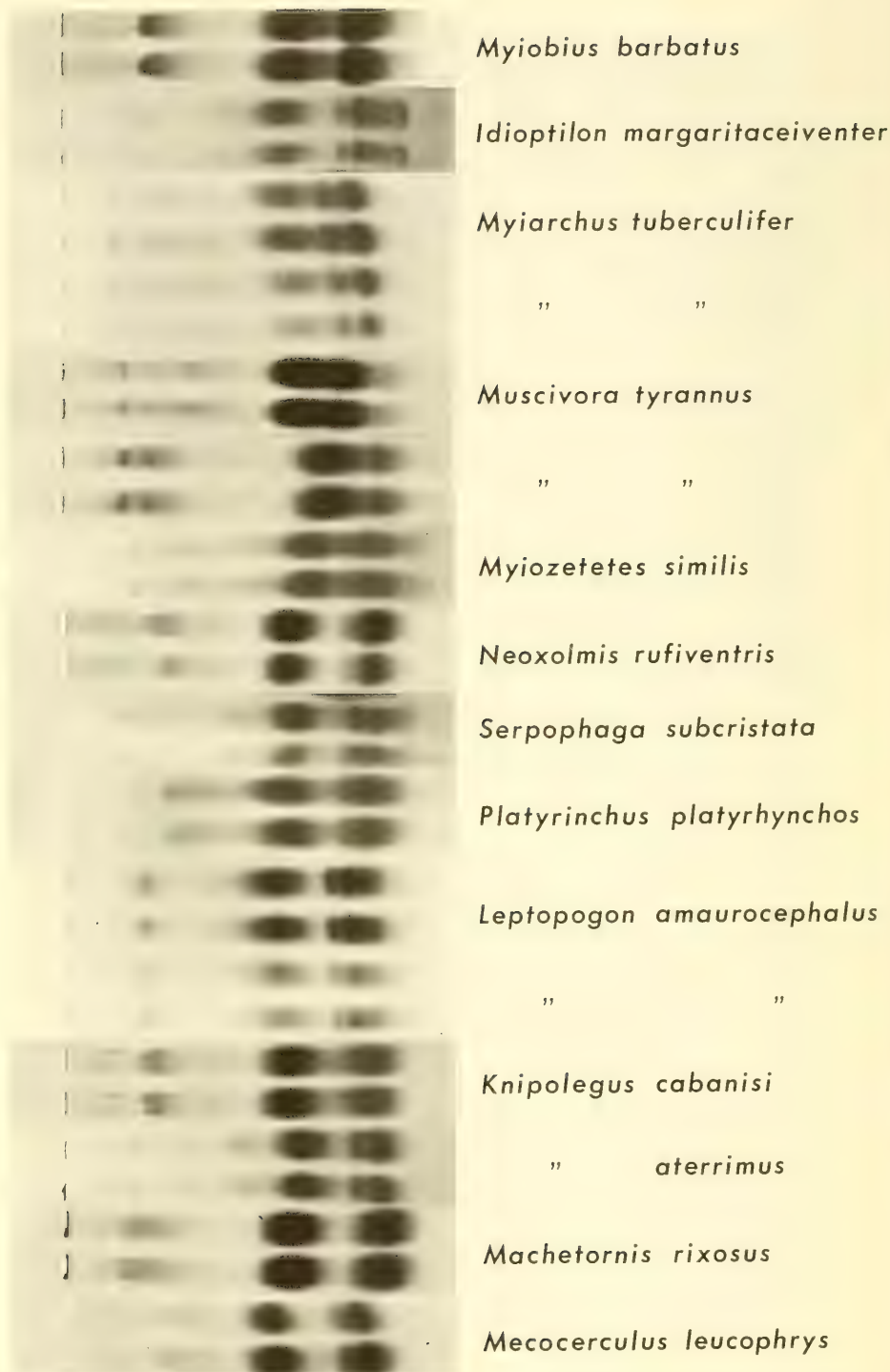


FIGURE 6. Starch gel electrophoretic patterns of the Tyrannidae (part).

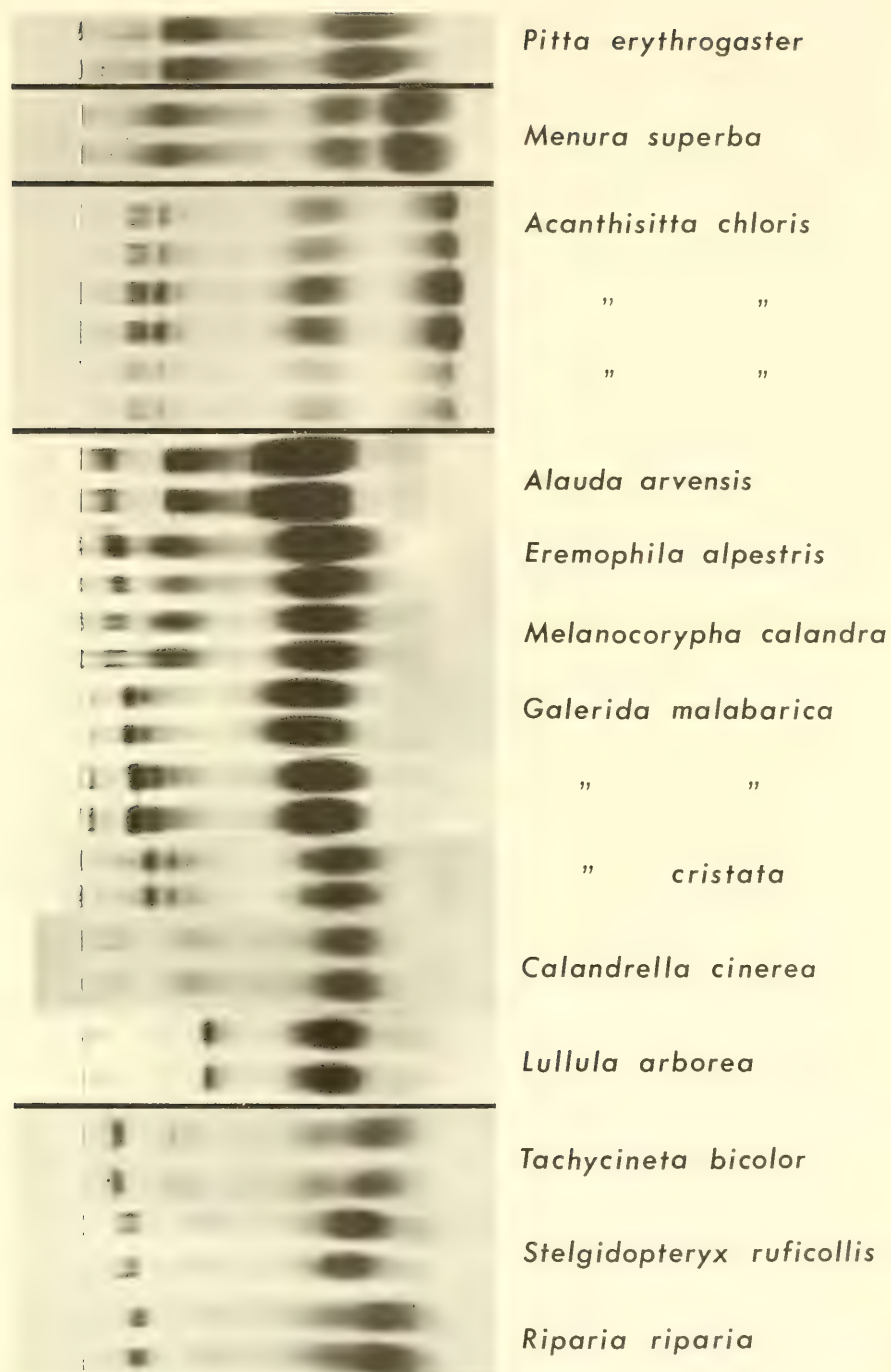


FIGURE 7. Starch gel electrophoretic patterns of the Pittidae, Menuridae, Acanthisittidae, Alaudidae and Hirundinidae (part).

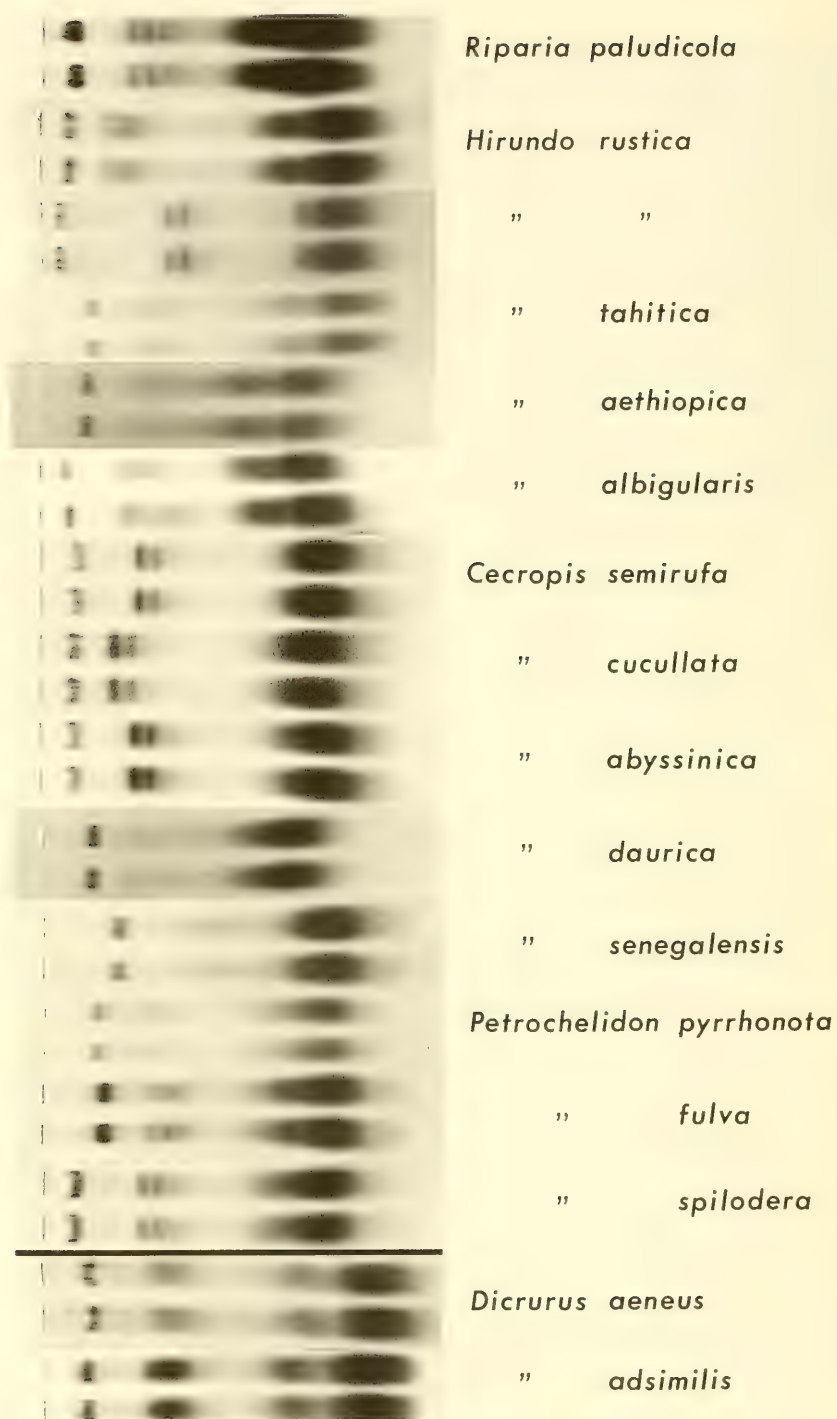


FIGURE 8. Starch gel electrophoretic patterns of the Hirundinidae (part) and Dicruridae (part).

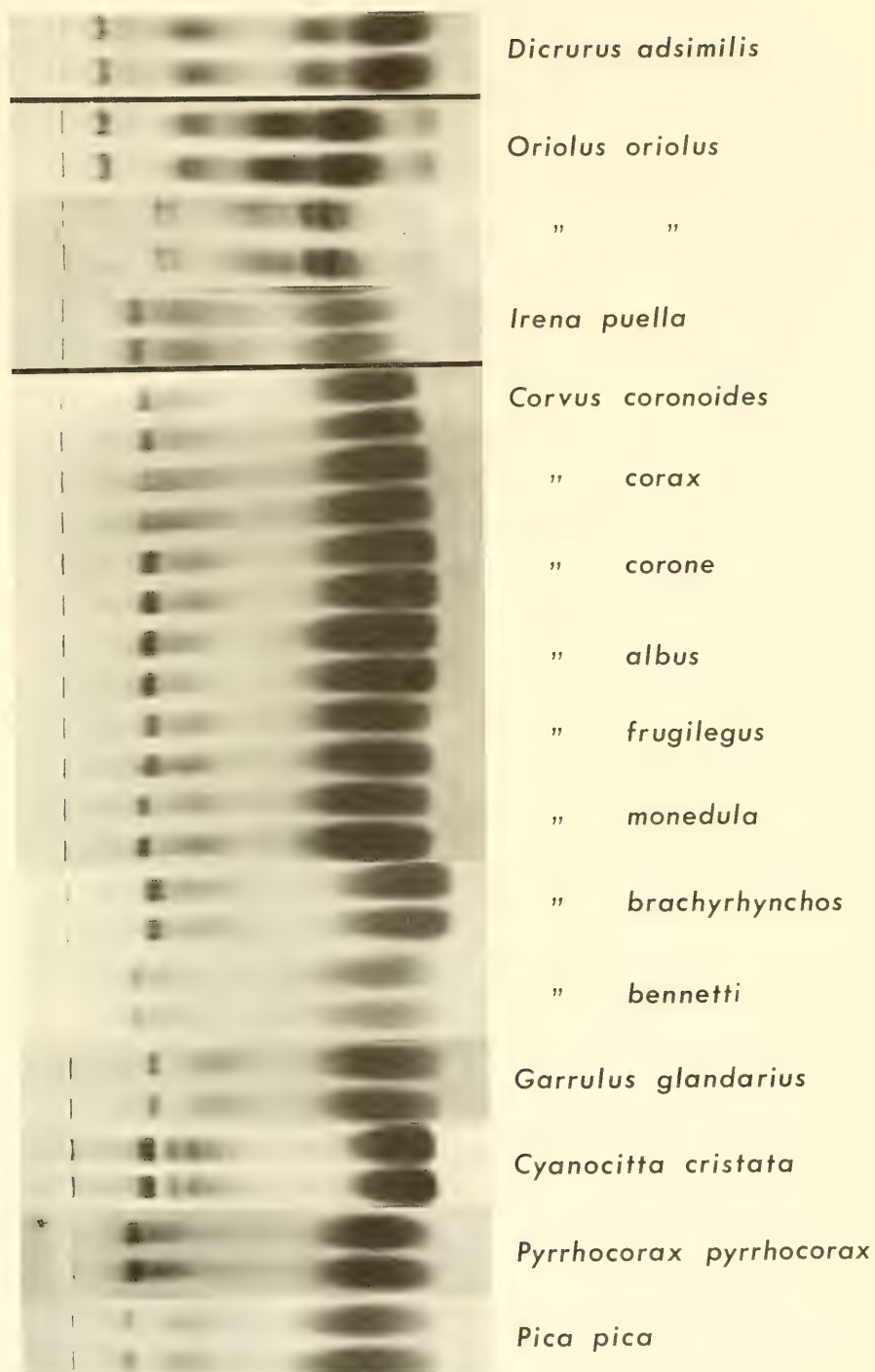


FIGURE 9. Starch gel electrophoretic patterns of the Dicruridae (part), Oriolidae and Corvidae (part).

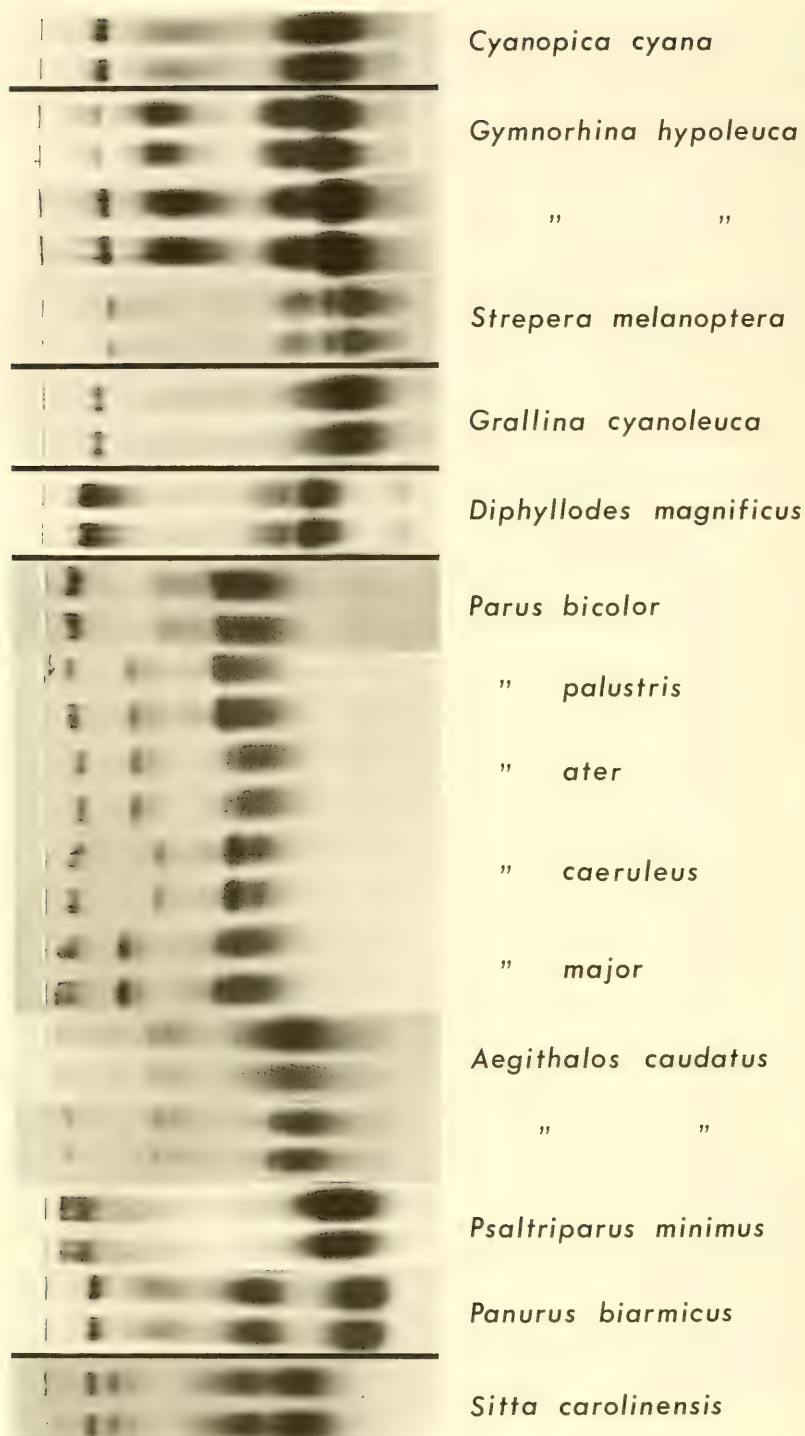


FIGURE 10. Starch gel electrophoretic patterns of the Corvidae (part), Cracti-
cidae, Grallinidae, Paradiseidae, Paridae and Sittidae (part).

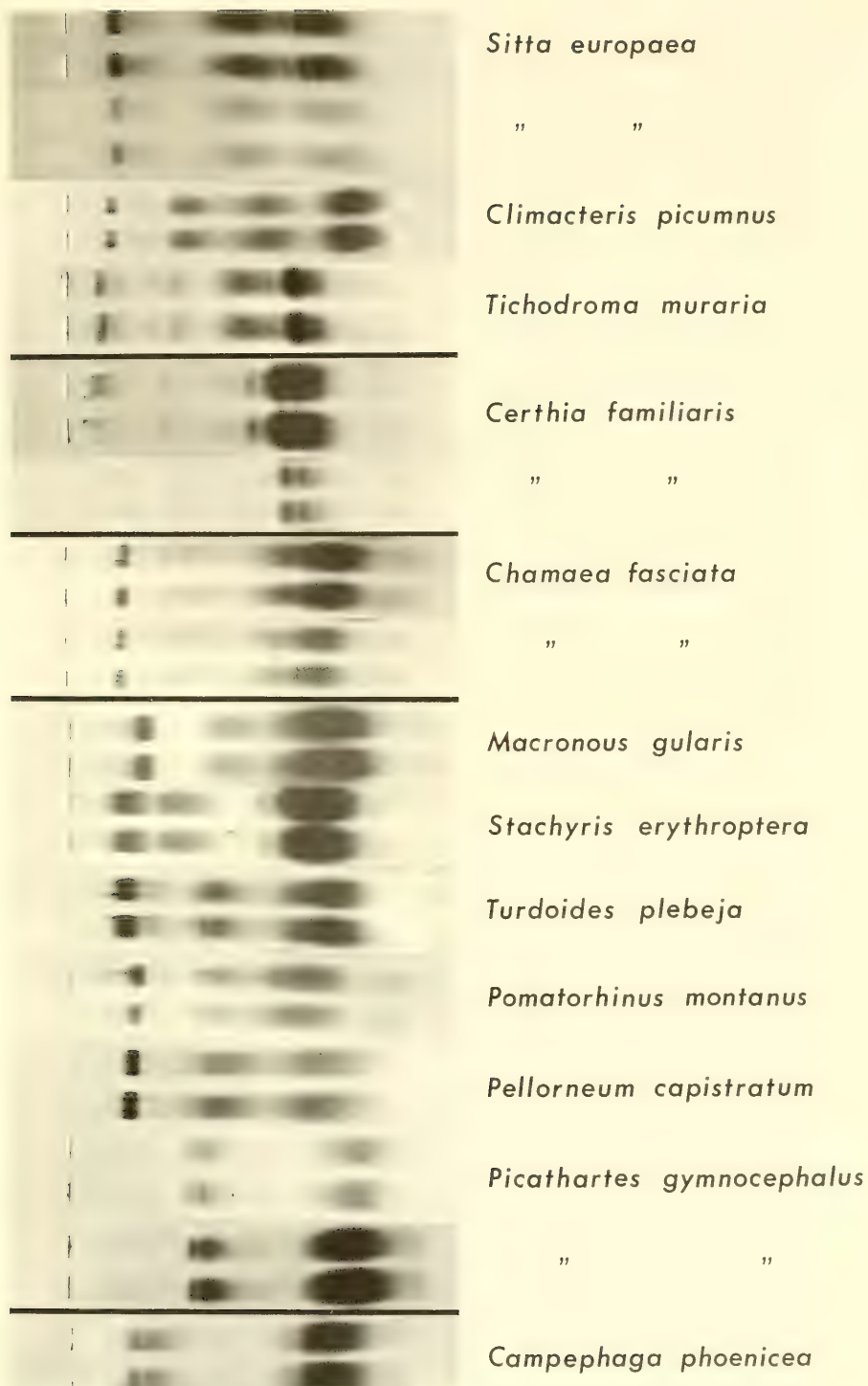


FIGURE 11. Starch gel electrophoretic patterns of the Sittidae (part), Certhiidae, Chamaeidae, Timaliidae and Campephagidae (part).

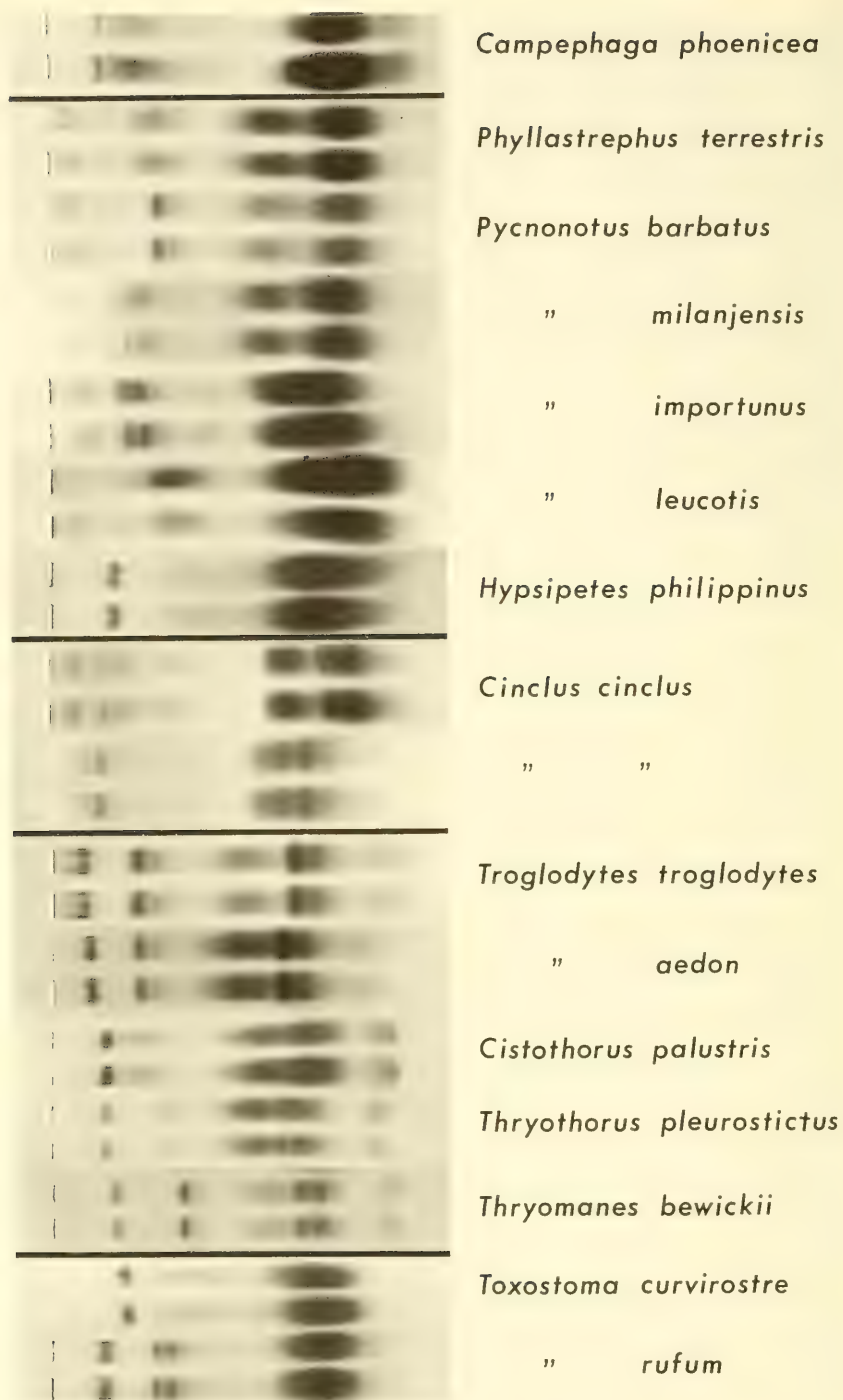


FIGURE 12. Starch gel electrophoretic patterns of the Campephagidae (part), Pycnonotidae, Cinclidae, Troglodytidae and Mimidae (part).

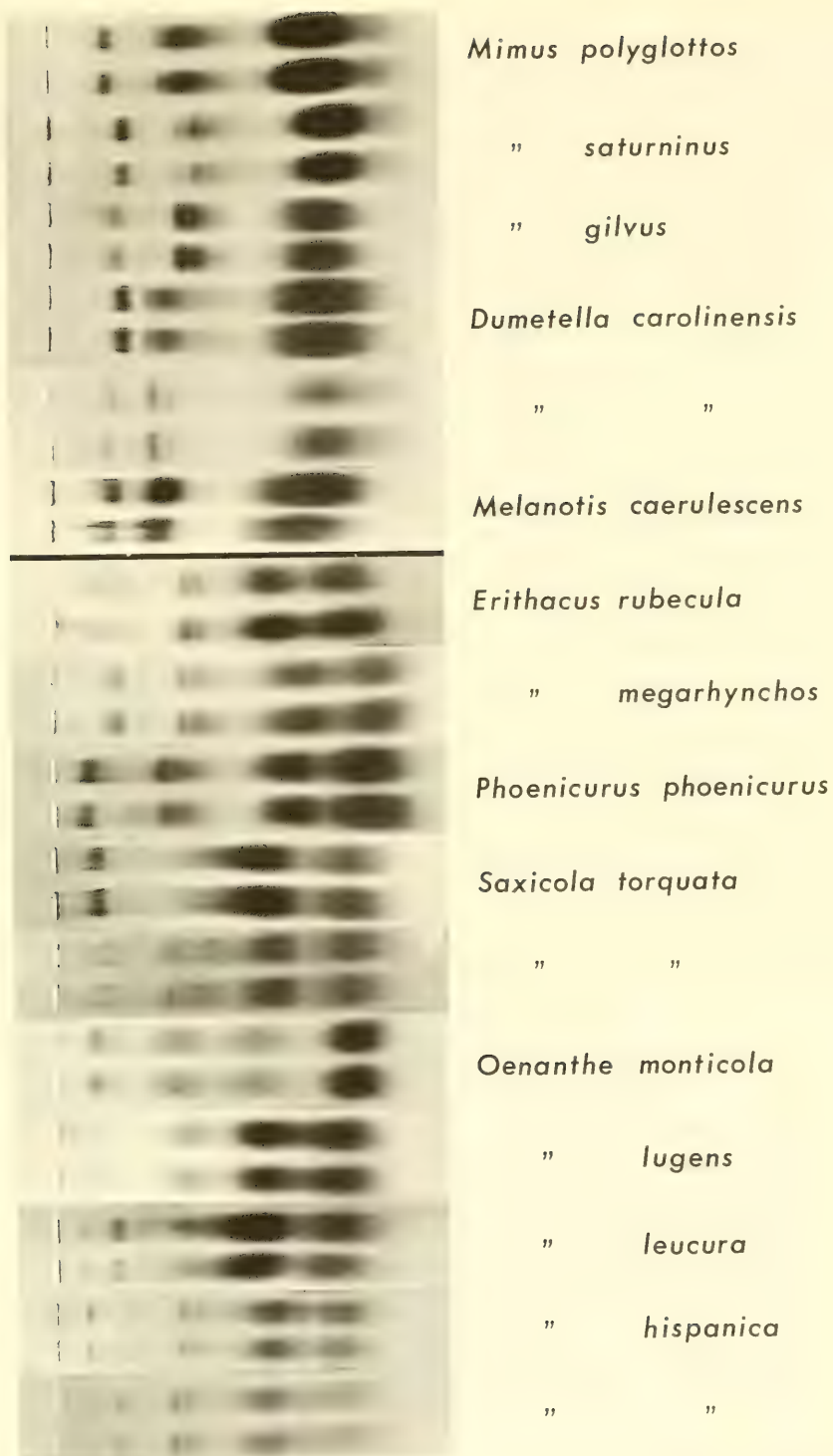


FIGURE 13. Starch gel electrophoretic patterns of the Mimidae (part) and Turdidae (part).

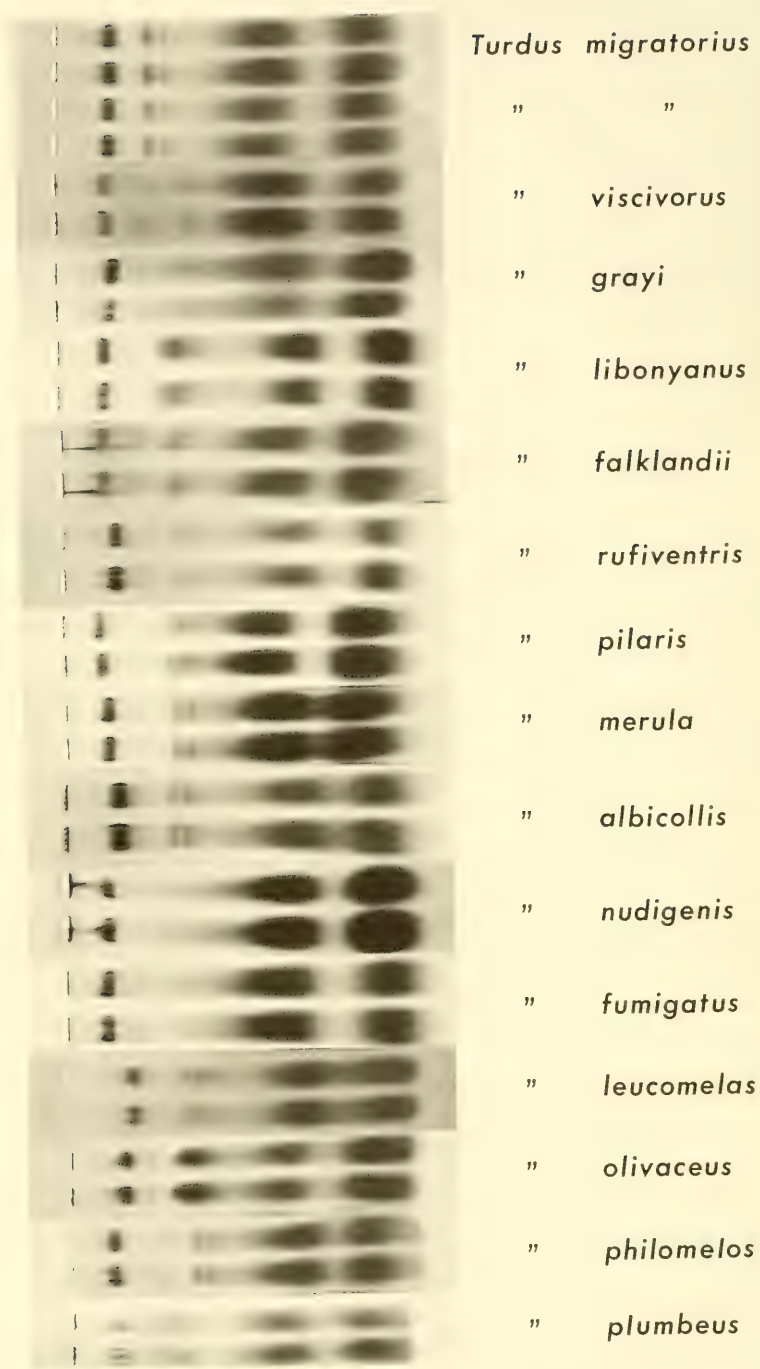


FIGURE 14. Starch gel electrophoretic patterns of the Turdidae (part).

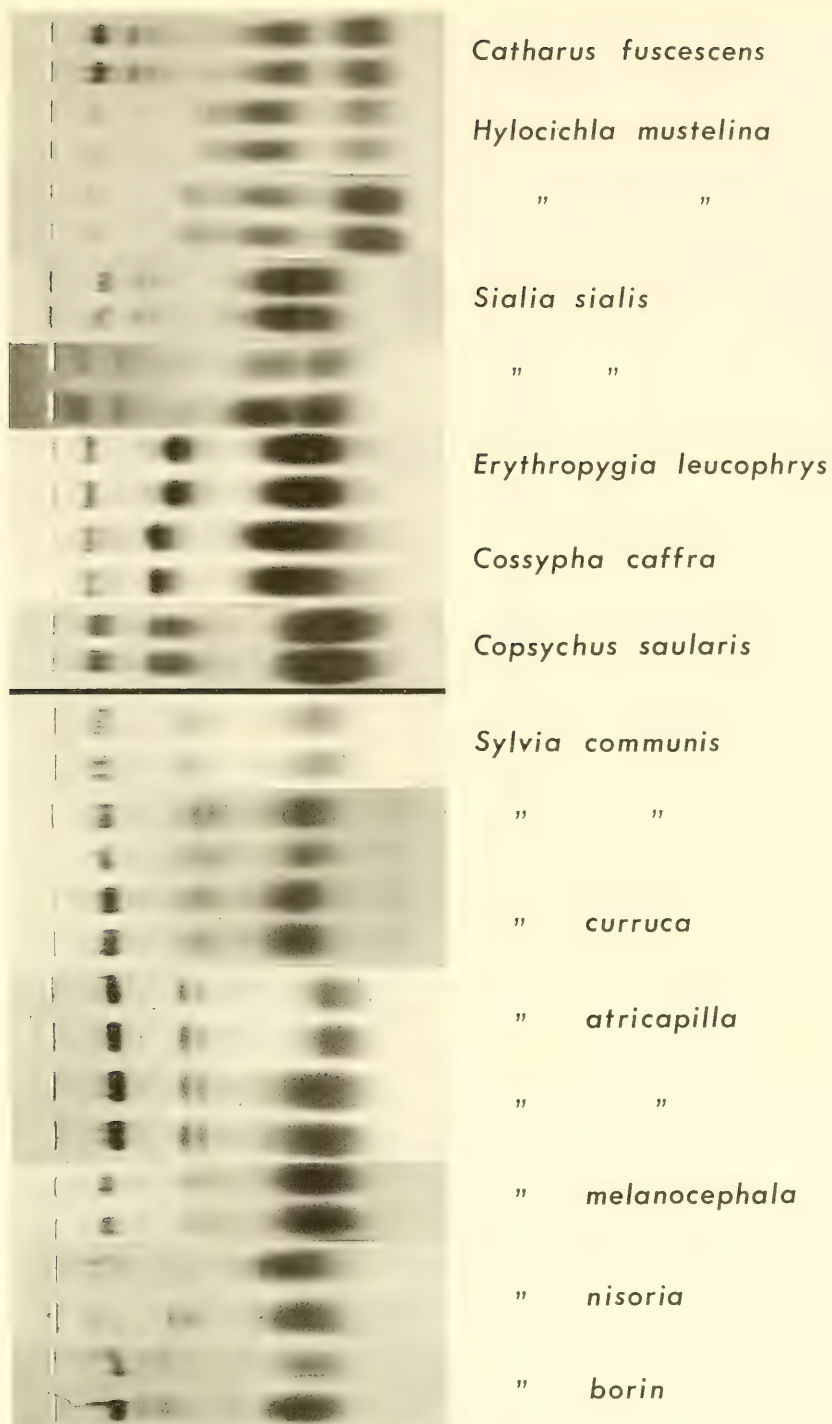


FIGURE 15. Starch gel electrophoretic patterns of the Turdidae (part) and Sylviidae (part).

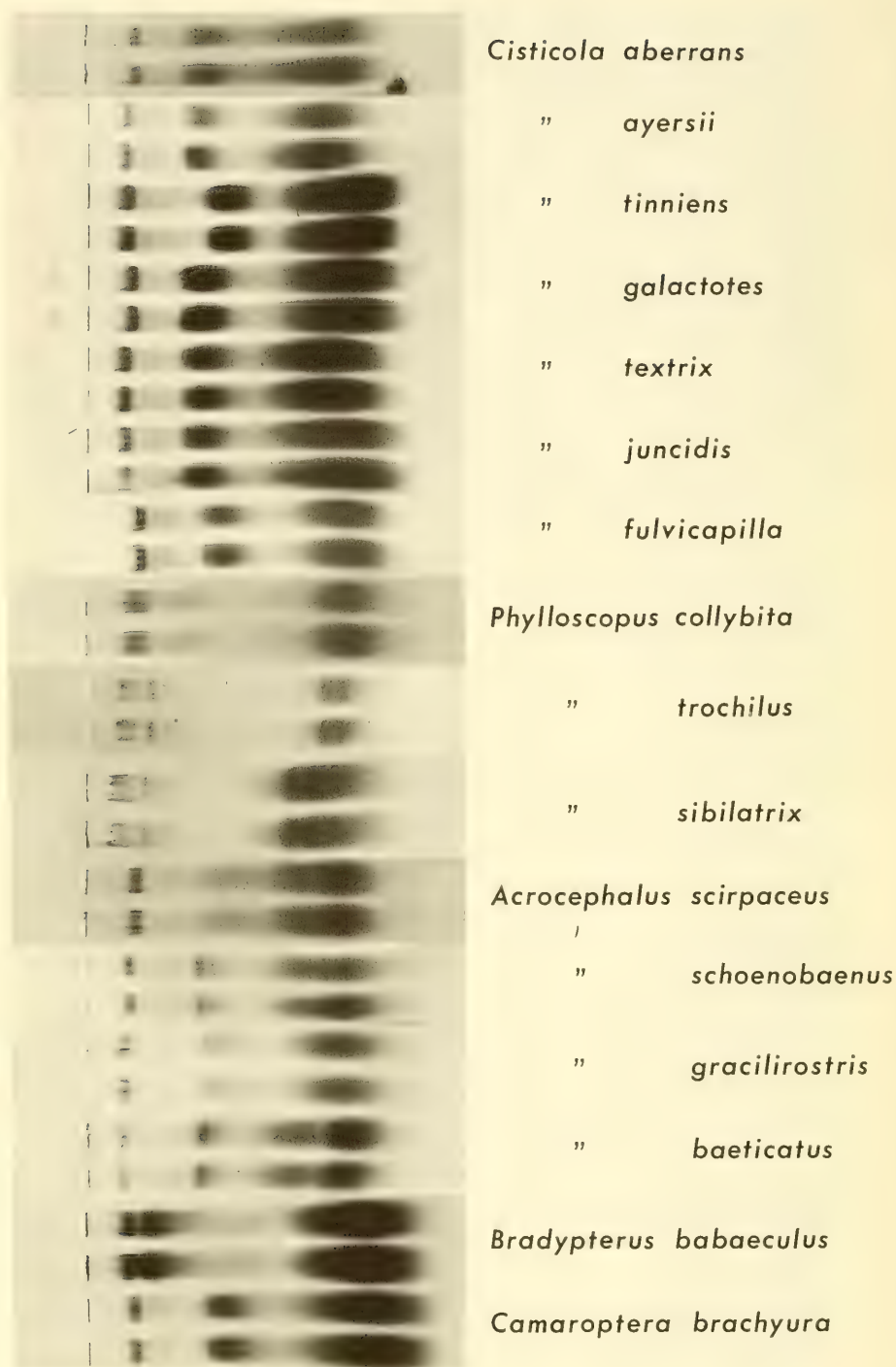


FIGURE 16. Starch gel electrophoretic patterns of the Sylviidae (part).

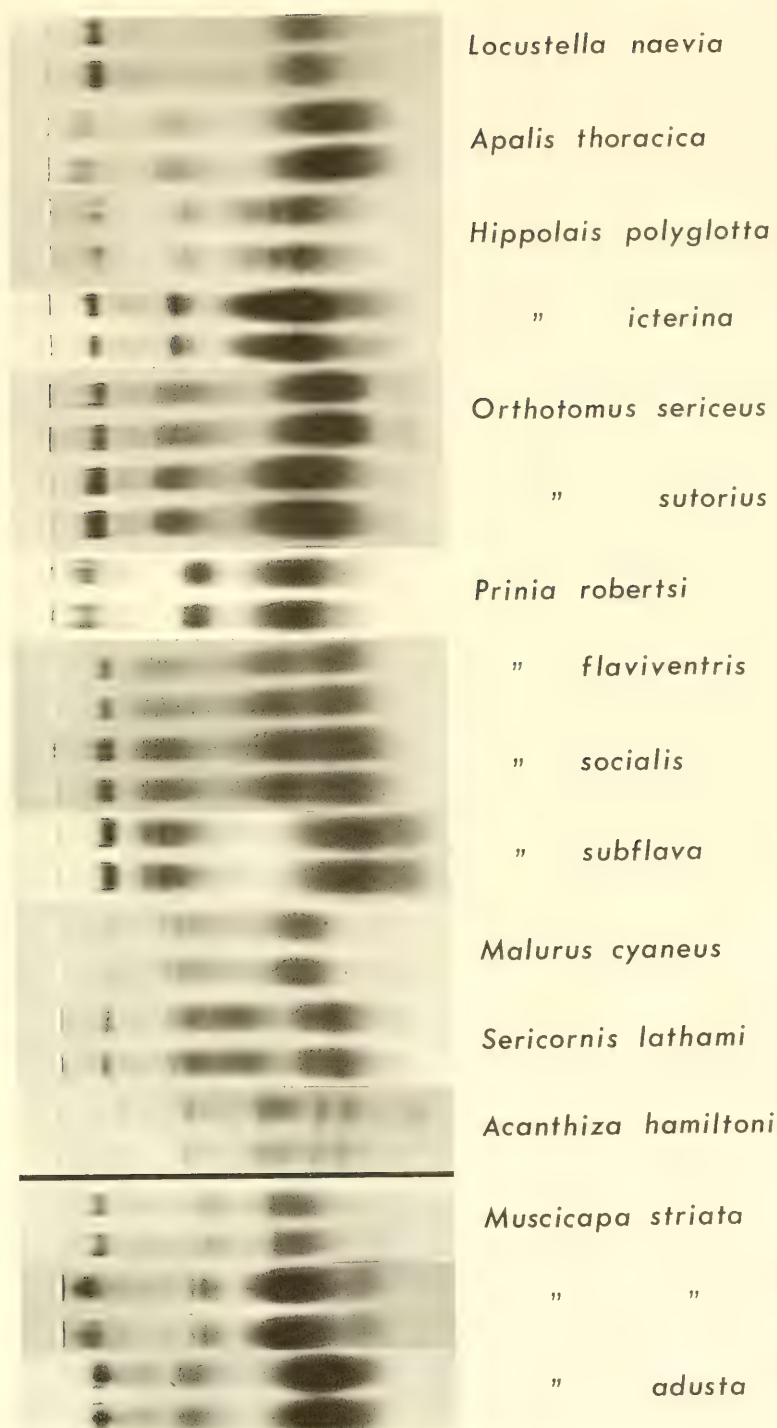


FIGURE 17. Starch gel electrophoretic patterns of the Sylviidae (part) and Muscicapidae (part).

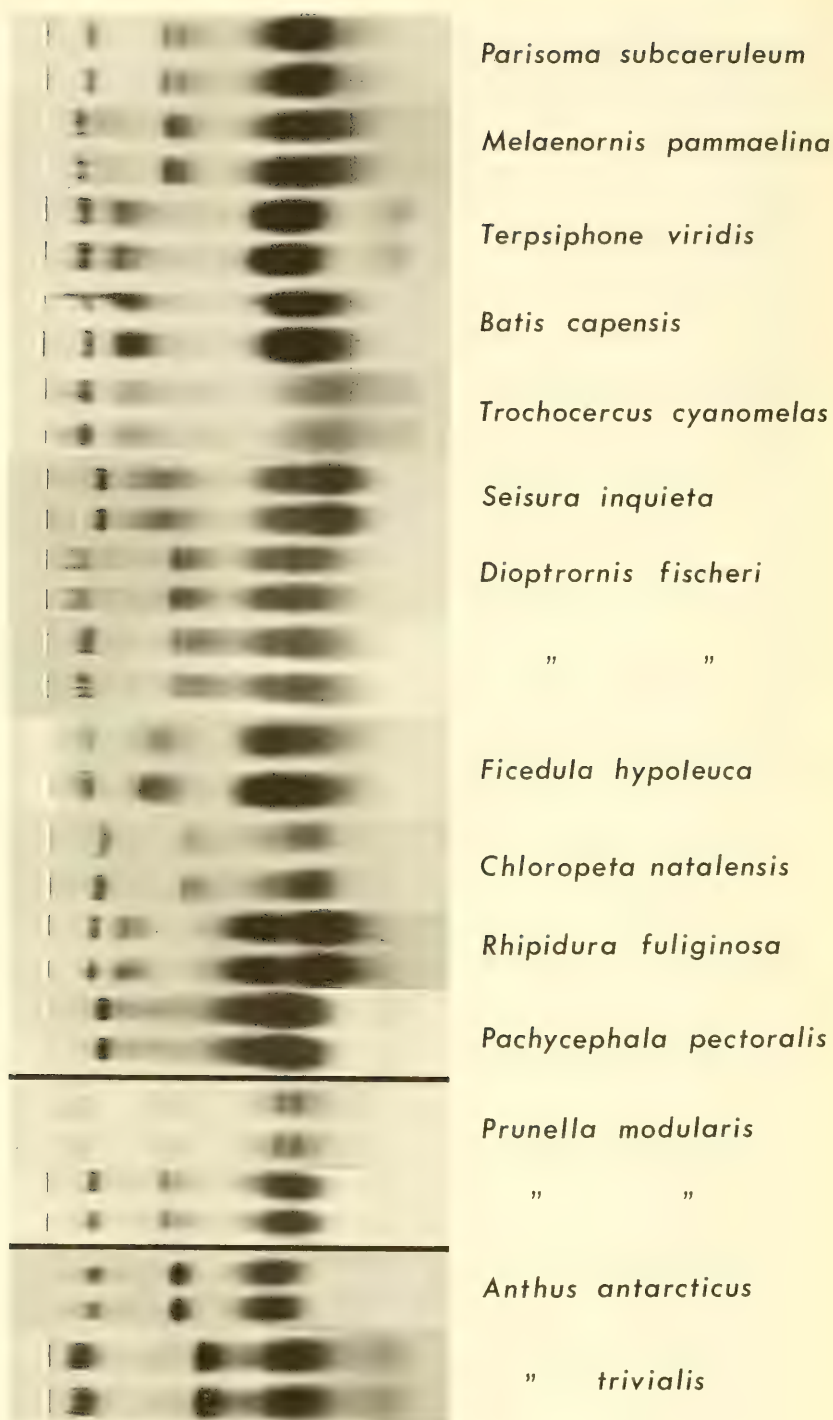


FIGURE 18. Starch gel electrophoretic patterns of the Muscicapidae (part), Prunellidae and Motacillidae (part).

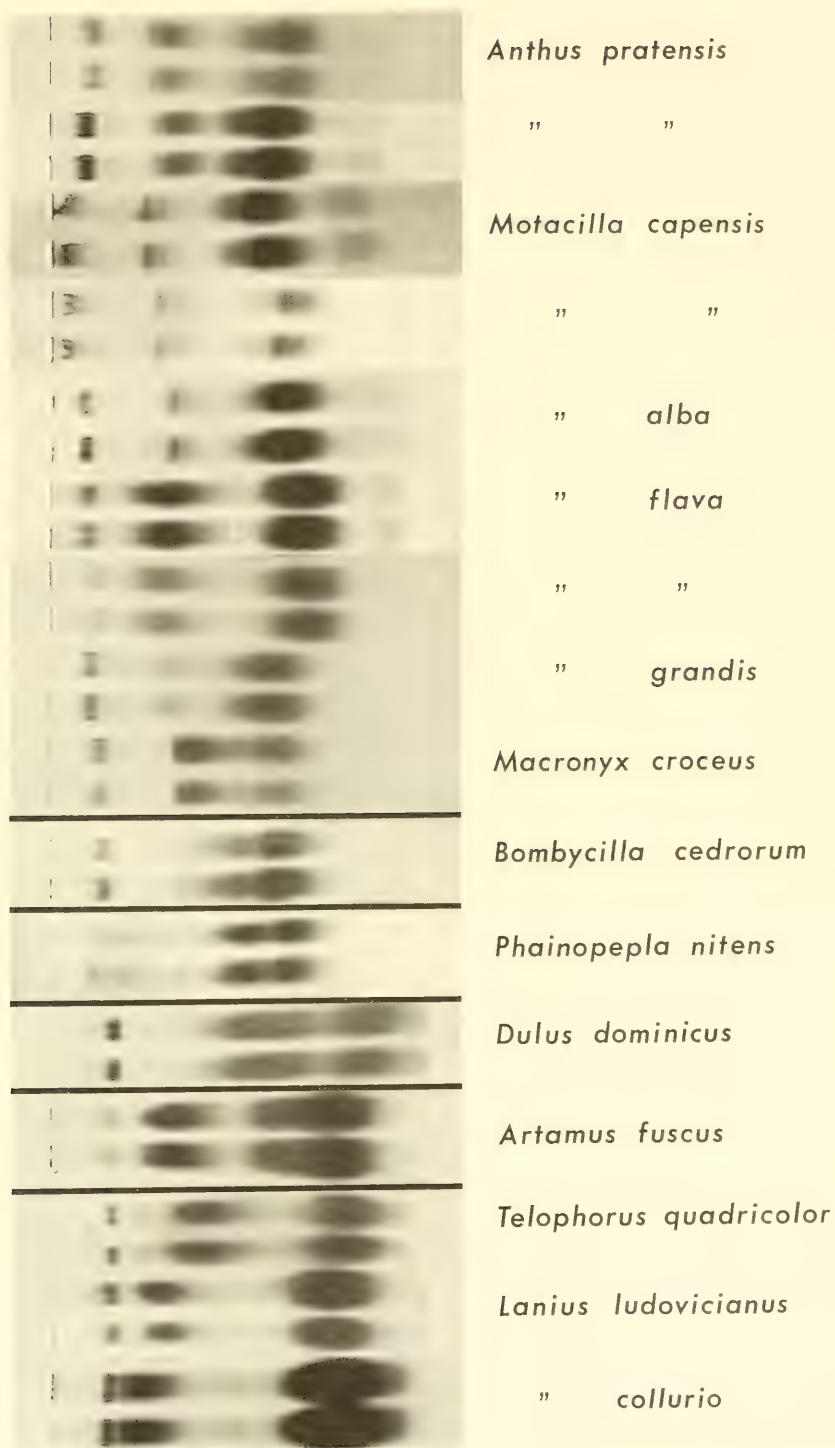


FIGURE 19. Starch gel electrophoretic patterns of the Motacillidae (part), Bombycillidae, Ptilonotidae, Dulidae, Artamidae and Laniidae (part).

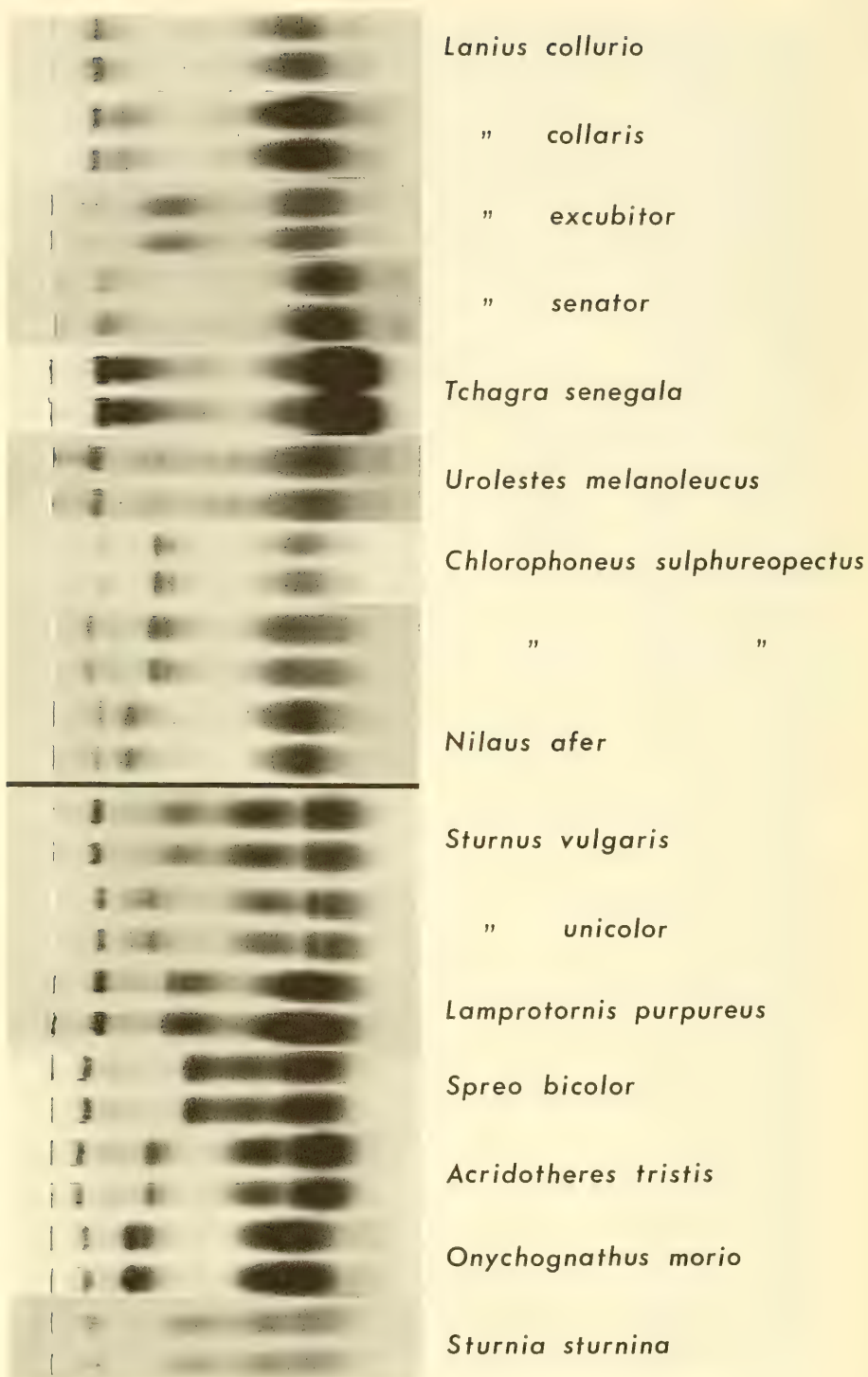


FIGURE 20. Starch gel electrophoretic patterns of the Laniidae (part) and Sturnidae.

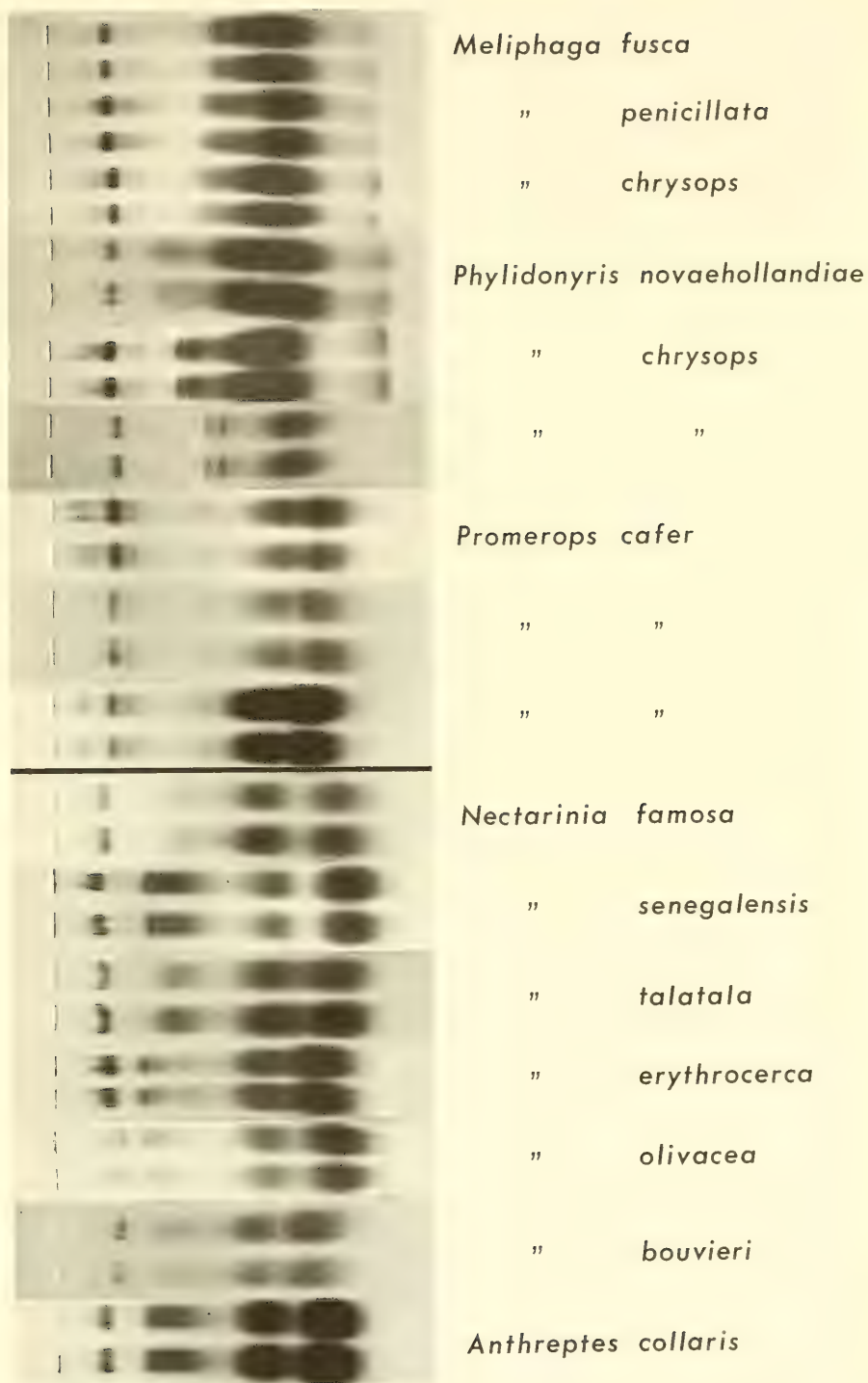


FIGURE 21. Starch gel electrophoretic patterns of the Meliphagidae and Nectariniidae.

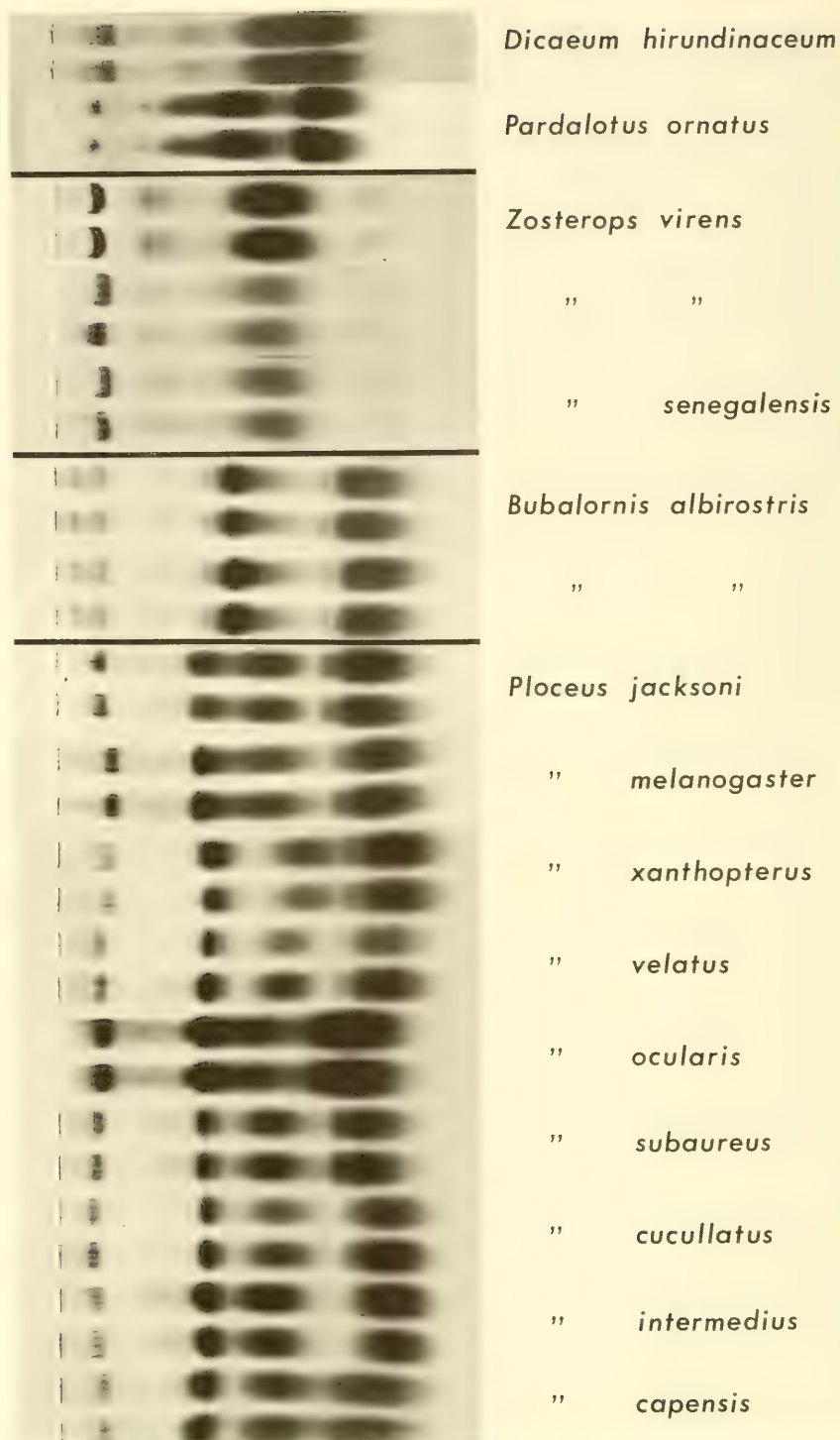


FIGURE 22. Starch gel electrophoretic patterns of the Dicaeidae, Zosteropidae, Bubalornithinae and Ploceinae (part).

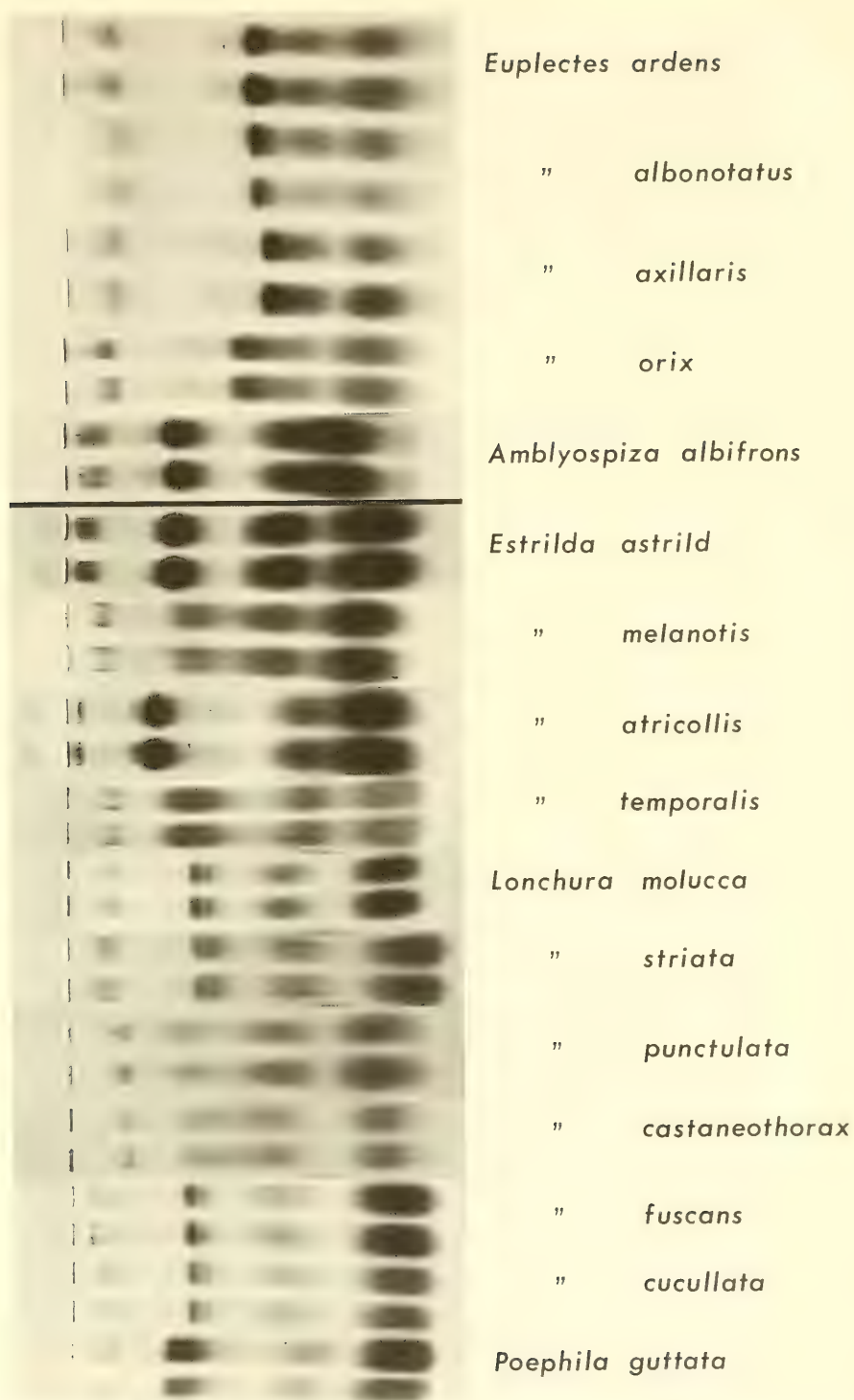


FIGURE 23. Starch gel electrophoretic patterns of the Ploceinae (part) and Estrildinae.

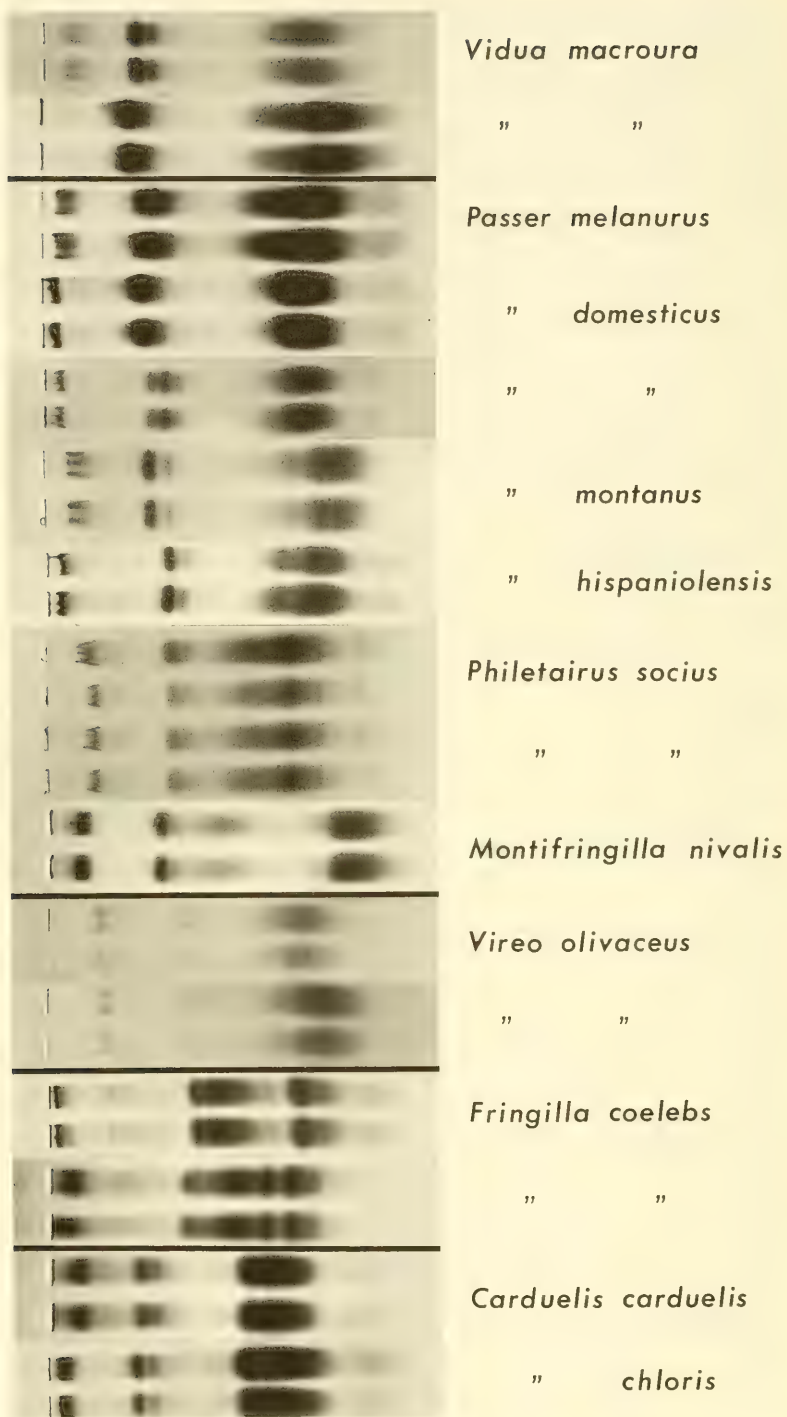


FIGURE 24. Starch gel electrophoretic patterns of the Viduinae, Passeridae, Vireonidae, Fringillini and Carduelini (part).

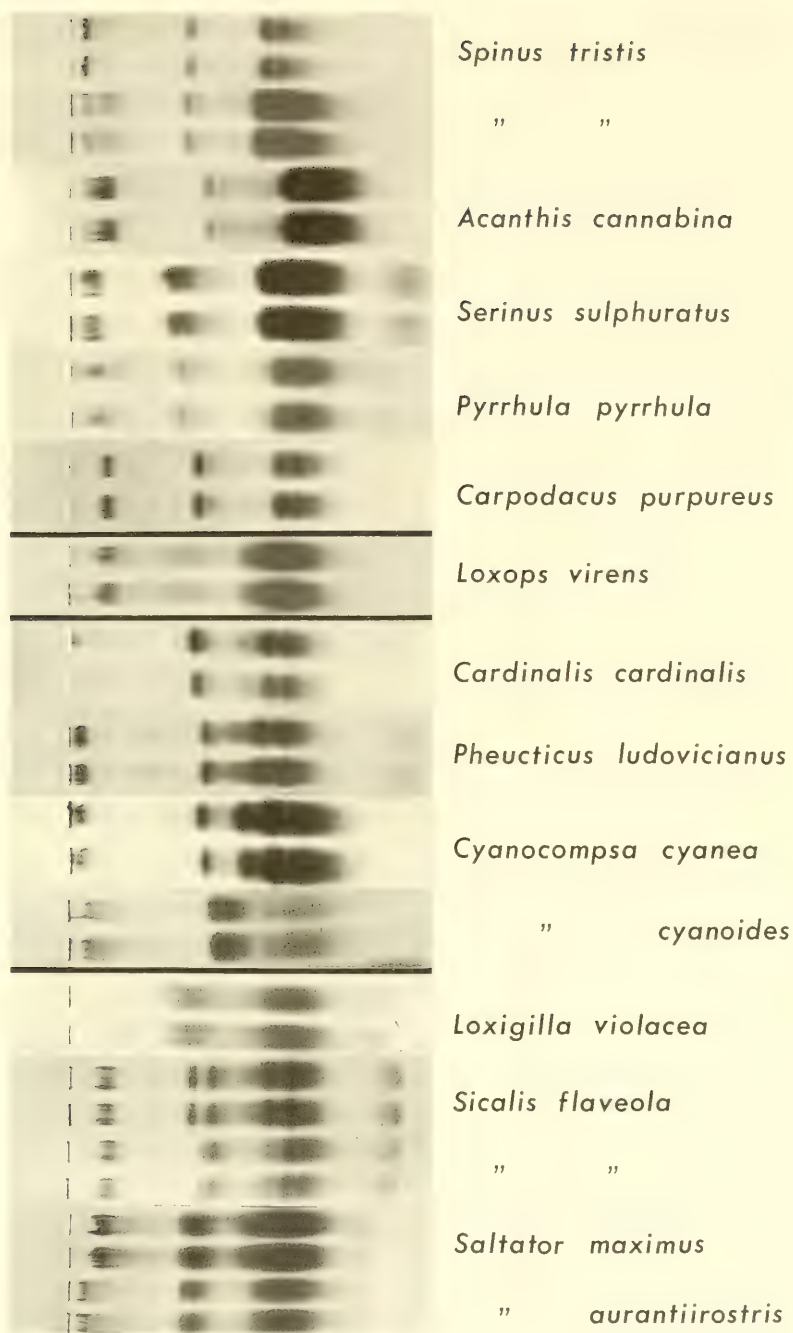


FIGURE 25. Starch gel electrophoretic patterns of the Carduelini (part), Drepaninini, Cardinalini and Emberizini (part).

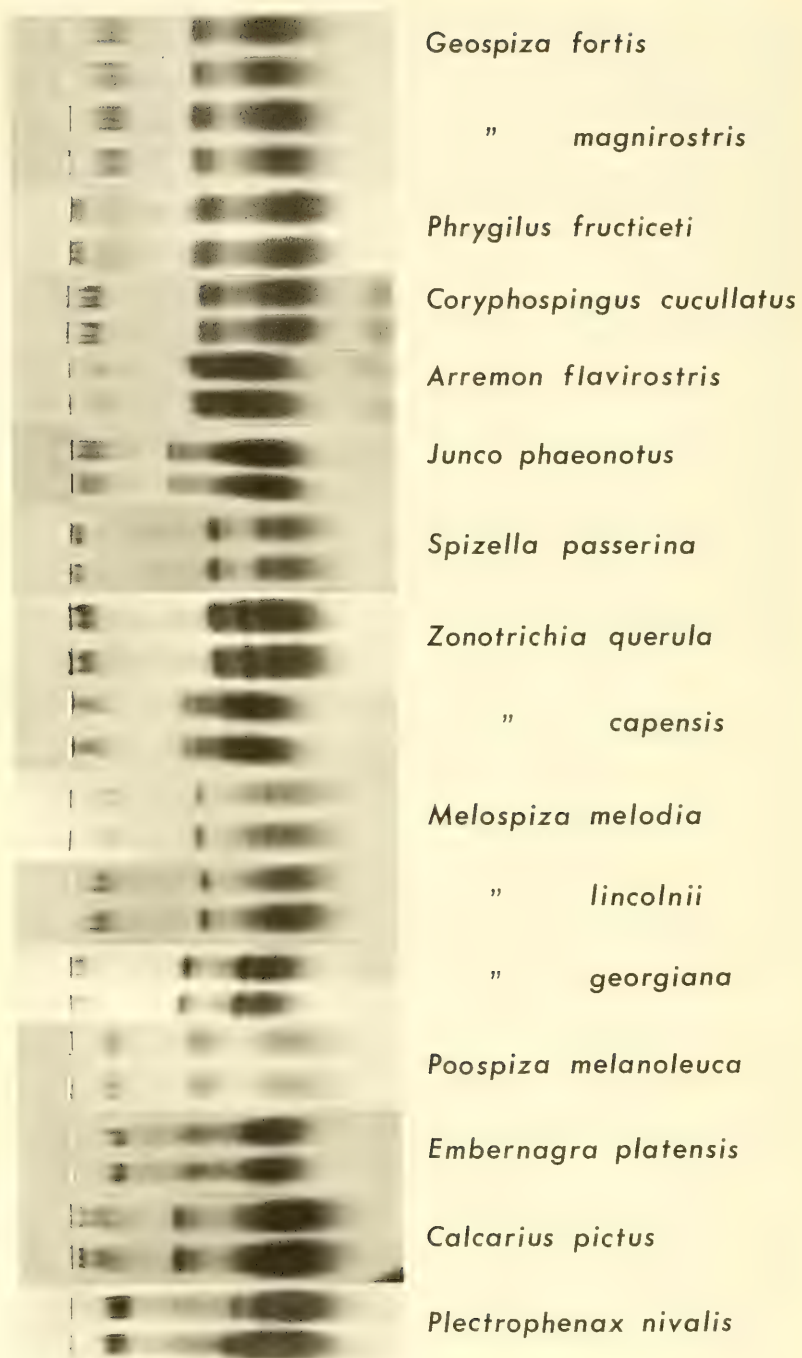


FIGURE 26. Starch gel electrophoretic patterns of the Emberizini (part).

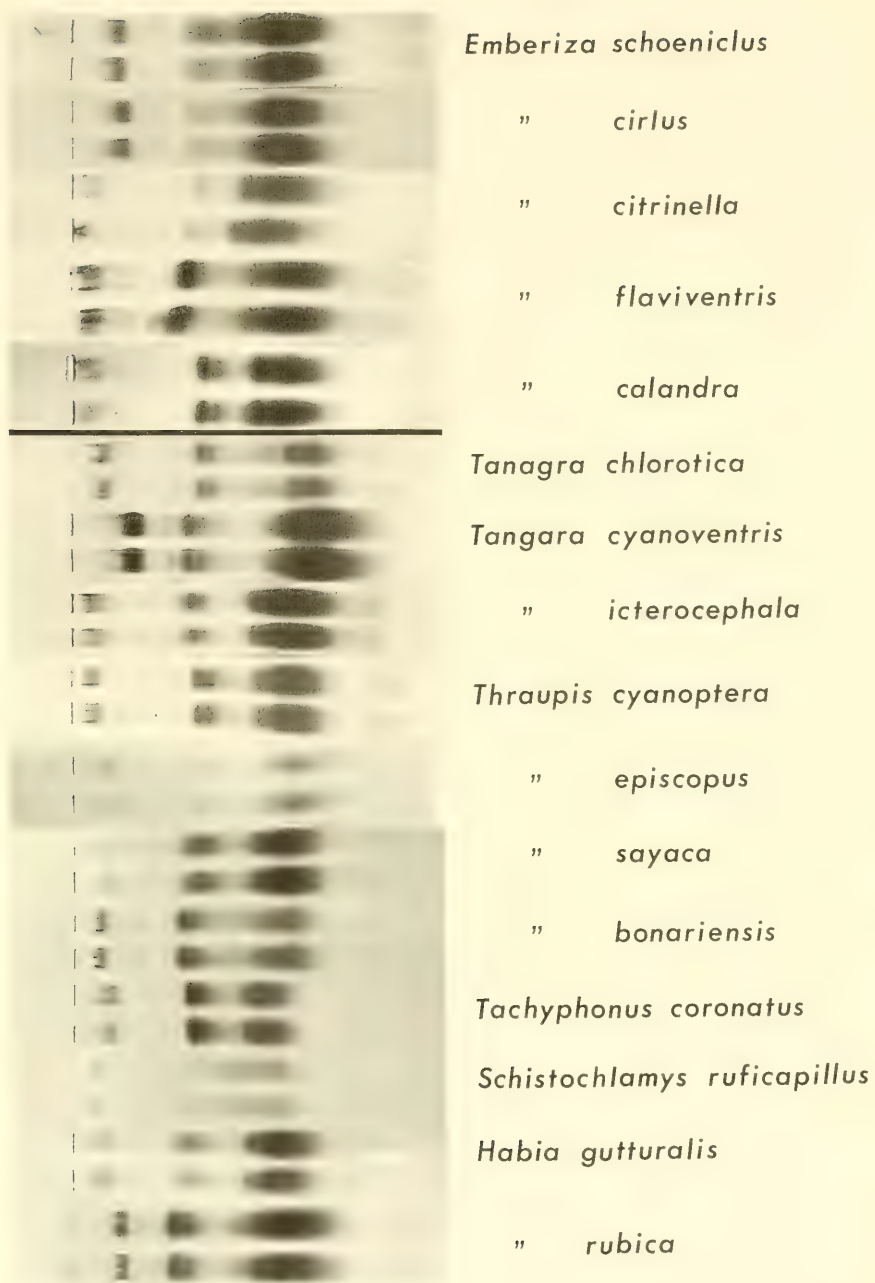


FIGURE 27. Starch gel electrophoretic patterns of the Emberizini (part) and Thraupini (part).

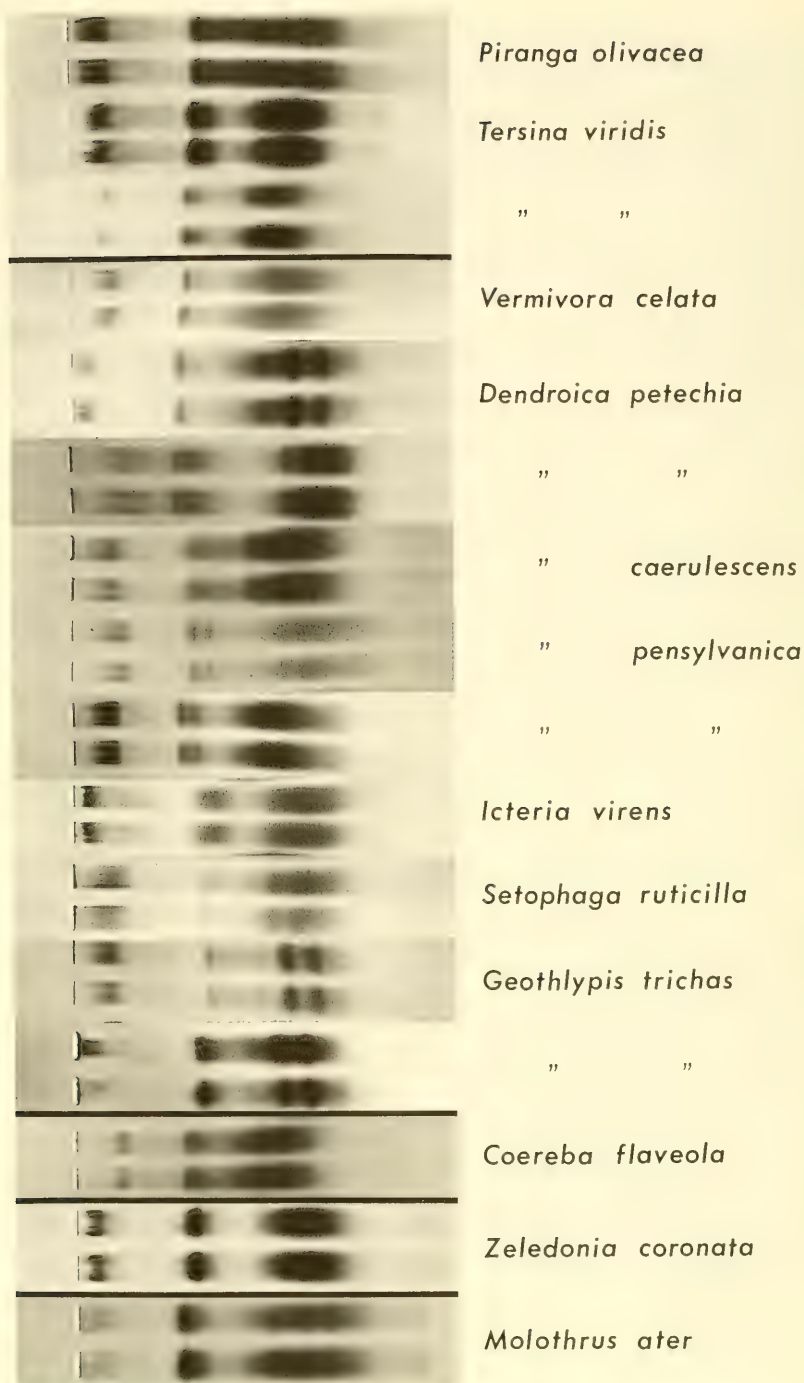


FIGURE 28. Starch gel electrophoretic patterns of the Thraupini (part), Parulini, Coerebini, Zeledoniini and Icterinae (part).

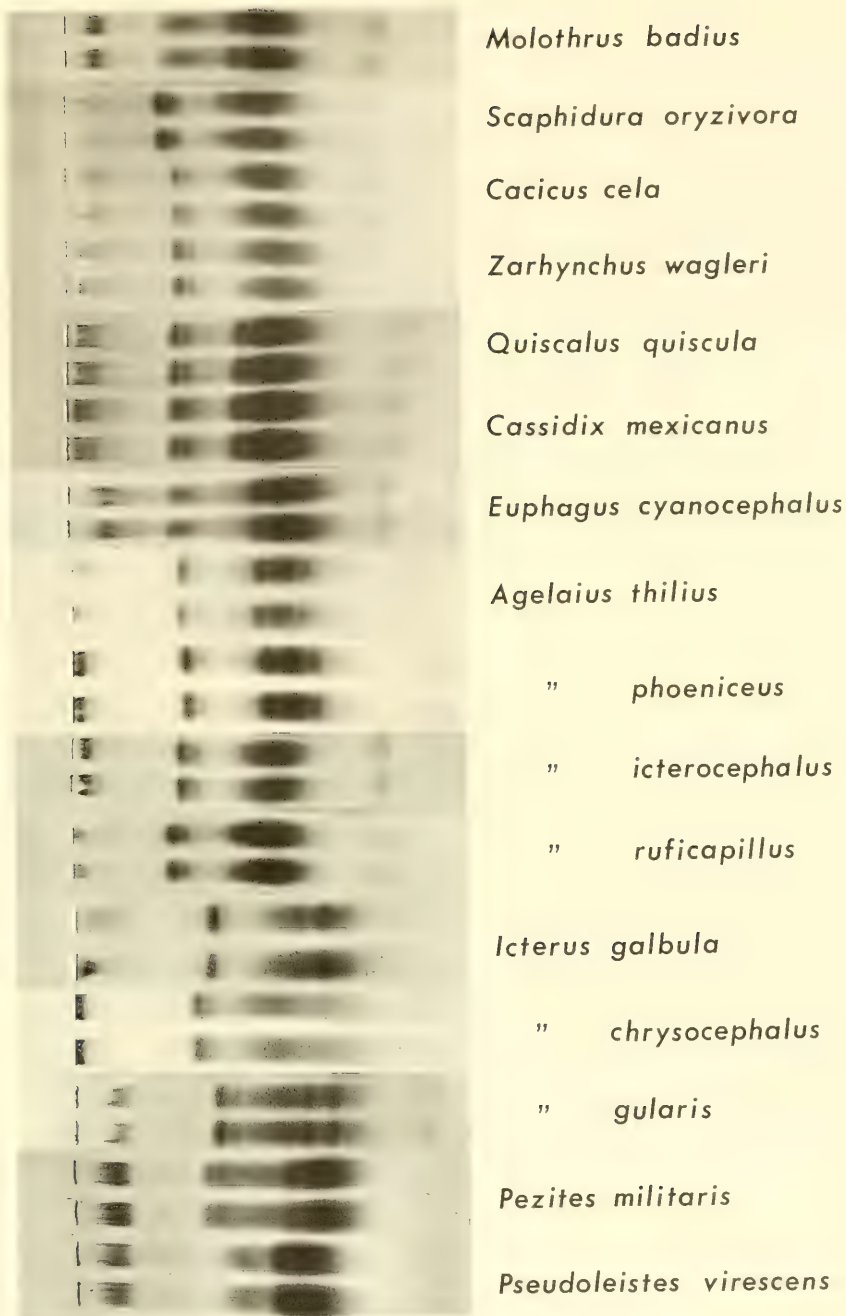
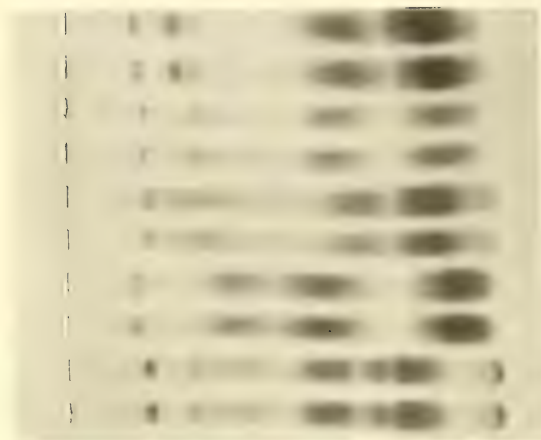


FIGURE 29. Starch gel electrophoretic patterns of the Icterinae (part).

S-239



Furnarius rufus

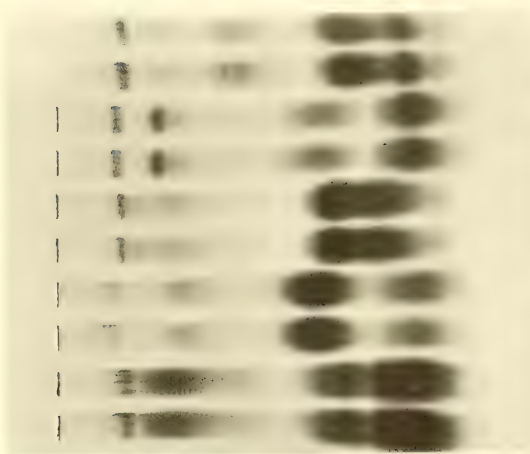
Synallaxis frontalis

" *brachyura*

Asthenes baeri

Geositta cunicularia

S-418



Thamnophilus doliatus

Furnarius rufus

Tyrannus tyrannus

Sayornis phoebe

Platypsaris aglaiae

FIGURE 30. Starch gel No. S-239 showing variation in the patterns of the Furnariidae and No. S-418 comparing the Formicariidae (*Thamnophilus*), Furnariidae (*Furnarius*), Tyrannidae (*Tyrannus*, *Sayornis*) and Cotingidae (*Platypsaris*).

S-435



Estrilda temporalis

Passer domesticus

Poephila guttata

Vidua macroura

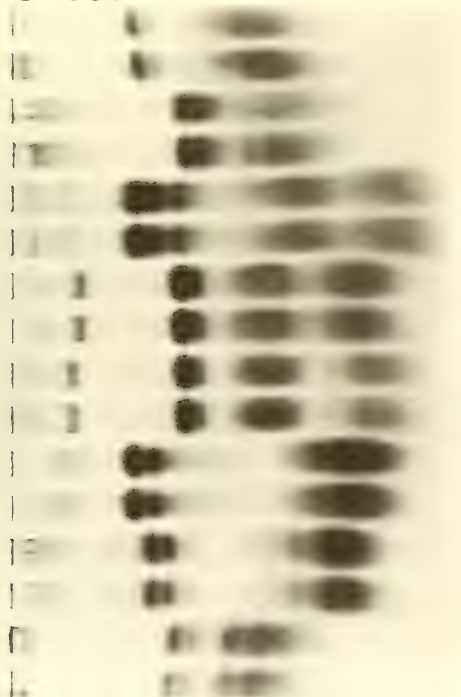
Lonchura striata

Poephila guttata

Spinus tristis

Melospiza georgiana

S-661



Agelaius icterocephalus

Cyanocompsa cyanooides

Poephila guttata

Ploceus capensis

" *jacksoni*

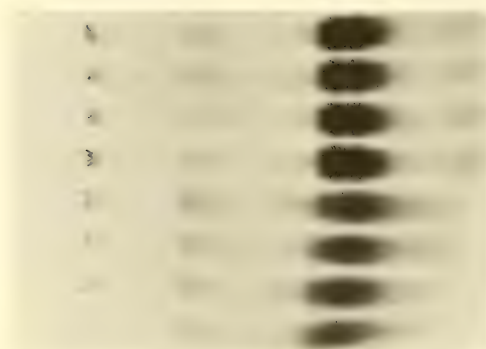
Vidua macroura

Passer melanurus

Spizella passerina

FIGURE 31. Starch gel No. S-435 comparing several estrildines (*Estrilda*, *Poephila*, *Lonchura*) with *Vidua*, *Passer*, a cardueline (*Spinus*) and an emberizine (*Melospiza*). No. S-661 comparing several fringillids (*Agelaius*, *Cyanocompsa*, *Spizella*), ploceids (*Ploceus*, *Poephila*), *Vidua* and *Passer*.

S-1830



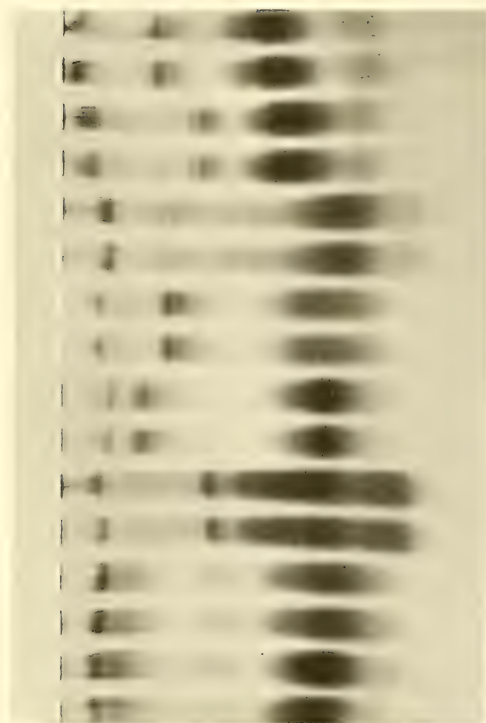
Certhia familiaris

" "

Aegithalos caudatus

" "

S-1986



Motacilla capensis

Muscicapa striata

Urolestes melanoleucus

Chlorophoneus sulphureopectus

Nilais afer

Laniarius ferrugineus

Lanius collurio

" *senator*

FIGURE 32. Starch gel No. S-1830 demonstrating the similarities between the egg-white proteins of *Certhia* and *Aegithalos*. No. S-1986 indicates the similarity between the Motacillidae and Muscicapidae and the variation within the Laniidae.

S-2088



Dendroica petechia

Agelaius thilius

Pheucticus ludovicianus

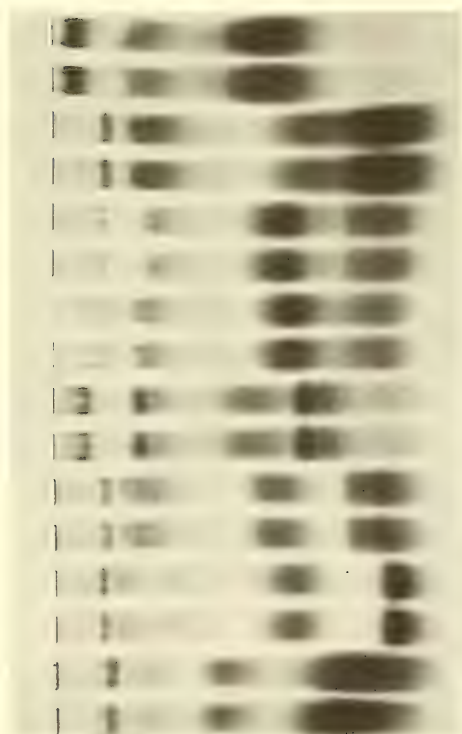
Fringilla coelebs

Cardinalis cardinalis

Zonotrichia capensis

Carduelis carduelis

S-2207



Parus major

Furnarius rufus

Sayornis phoebe

Knipolegus cabanisi

Troglodytes aedon

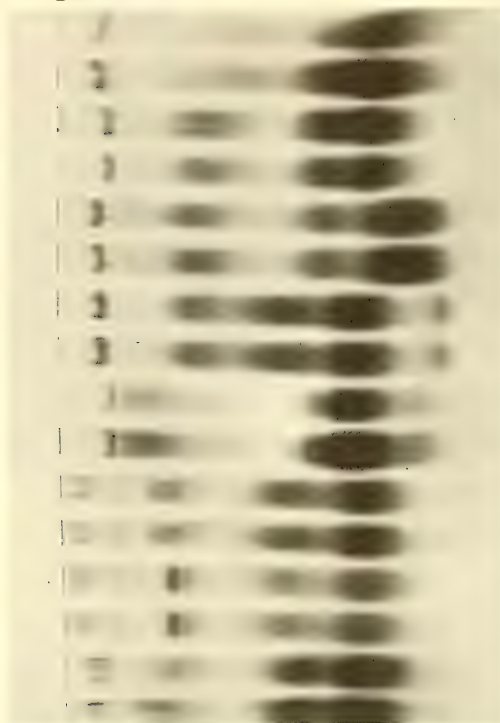
Synallaxis frontalis

Asthenes humicola

Thamnophilus caerulescens

FIGURE 33. Starch gel No. S-2088 to demonstrate similarities and differences within the Fringillidae. No. S-2207 compares a wren (*Troglodytes*) with *Parus* and with representatives of several groups of non-oscine passerines.

S-2213



Grallina cyanoleuca

Gymnorhina tibicen

Dicrurus adsimilis

Oriolus oriolus

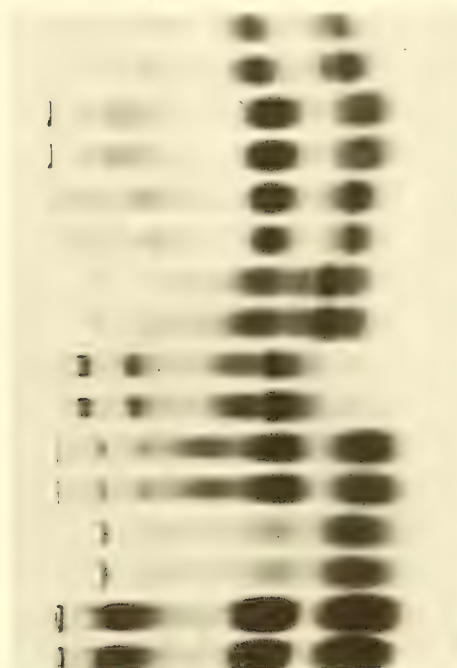
Campephaga phoenicea

Phyllastrephus terrestris

Pycnonotus barbatus

" *milanjensis*

S-2216



Mecocerculus leucophrys

Machetornis rixosus

Neoxolmis rufiventris

Elaenia flavogaster

Troglodytes aedon

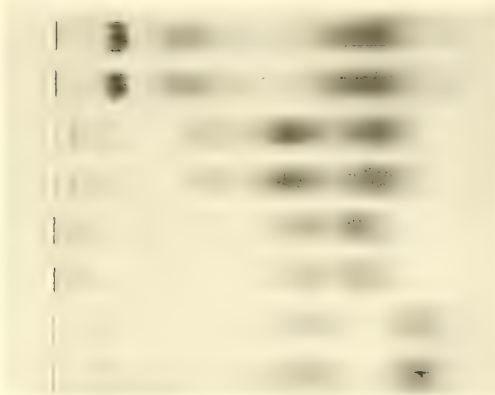
Synallaxis frontalis

Cranioleuca pyrrhophia

Phacellodomus rufifrons

FIGURE 34. Starch gel No. S-2213 comparing patterns of the Grallinidae, Cracticidae (*Gymnorhina*), Dicruridae, Oriolidae, Campephagidae and Pycnonotidae. S-2216 showing the similarities among several tyrannids and furnariids and the differences between them and *Troglodytes*.

S-2264



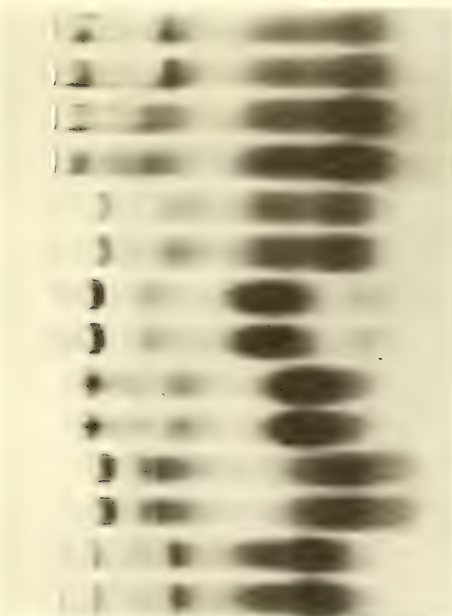
Prinia subflava

Oenanthe hispanica

Sialia sialis

Turdus migratorius

S-2281



Pycnonotus barbatus

Phyllastrephus terrestris

Nectarinia talatala

Zosterops virens

Muscicapa adusta

Prinia subflava

Acrocephalus baeticatus

FIGURE 35. Starch gel No. S-2264 showing the "ovomucoid" in the pattern of *Sialia* and comparing *Prinia* with three genera of the Turdidae. S-2281 comparing the Pycnonotidae (*Pycnonotus*, *Phyllastrephus*), Nectariniidae, Zosteropidae, Muscicapidae and Sylviidae (*Prinia*, *Acrocephalus*).

S-2272



Sylvia atricapilla

Prinia socialis

" *flaviventris*

" *subflava*

" *maculosa*

S-2381



Turdus merula

Phoenicurus phoenicurus

" *ochruros*

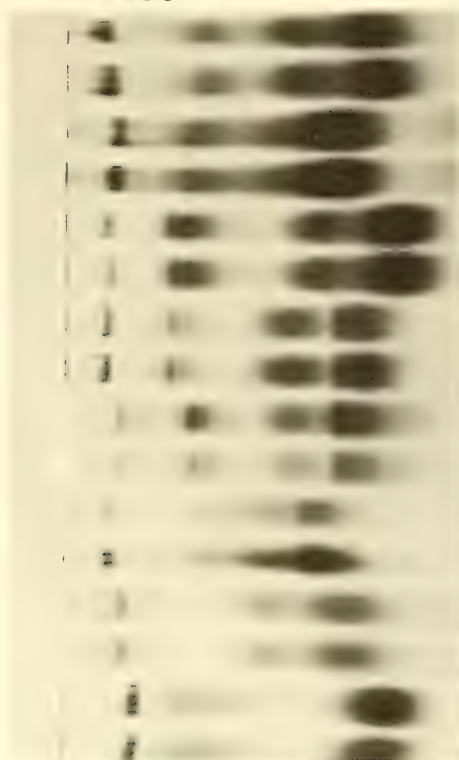
Oenanthe oenanthe

Cinclus cinclus

Acrocephalus scirpaceus

FIGURE 36. Starch gel No. S-2272 comparing *Sylvia* with four species of *Prinia*. No. S-2381 comparing *Cinclus* with several thrushes and a sylviid (*Acrocephalus*). Note the apparent "ovomucoid" fraction in *Acrocephalus*.

S-2386



Pycnonotus barbatus

Oriolus oriolus

Dicrurus adsimilis

Sturnus vulgaris

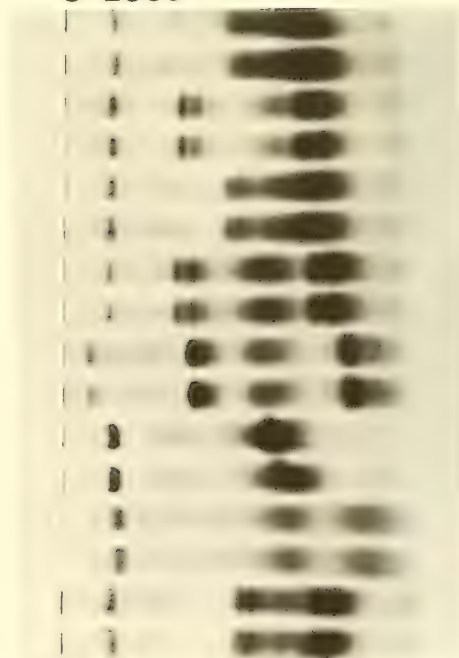
Artamus personatus

Bombycilla cedrorum

Meliphaga virescens

Cyanocitta cristata

S-2389



Meliphaga penicillata

Certhionyx variegatus

Phylidonyris albifrons

Lichmera indistincta

Pardalotus rubricatus

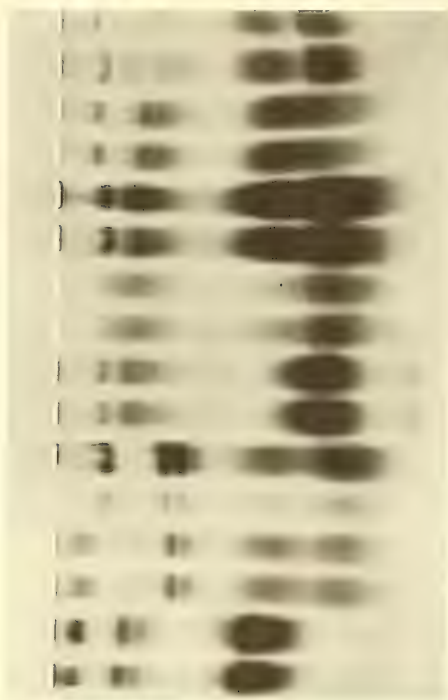
Zosterops palpebrosa

Nectarinia famosa

Phylidonyris albifrons

FIGURE 37. Starch gel No. S-2386 to show the similarity between the patterns of *Artamus* and *Sturnus* and between *Pycnonotus* and *Dicrurus*. No. S-2389 demonstrates the similarities among *Lichmera*, *Certhionyx* and *Pardalotus*, the differences between *Nectarinia* and the Meliphagidae and the differences between *Zosterops* and the meliphagids and nectariniids.

S-2450



Sturnus vulgaris
Ficedula hypoleuca
Rhipidura leucophrys
Sphenostoma cristatum
Colluricincla rufiventris
Stachyris poliocephala
Pycnonotus xanthopygos
Parus atricapillus

S-2451



Gymnorhina tibicen
Artamus personatus
Sturnus vulgaris
Sericornis lathamii
Acanthiza chrysorrhoa
Pardalotus rubricatus
Certhionyx variegatus
Lichmera indistincta

FIGURE 38. Starch gel No. S-2450 to demonstrate the differences between *Sphenostoma* and *Parus*. No. S-2451 indicates that the pattern of *Acanthiza* is similar to those of *Lichmera* and *Certhionyx*.



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